

# From species range-shifts to food-web alterations: consequences of global warming in the Mediterranean Sea

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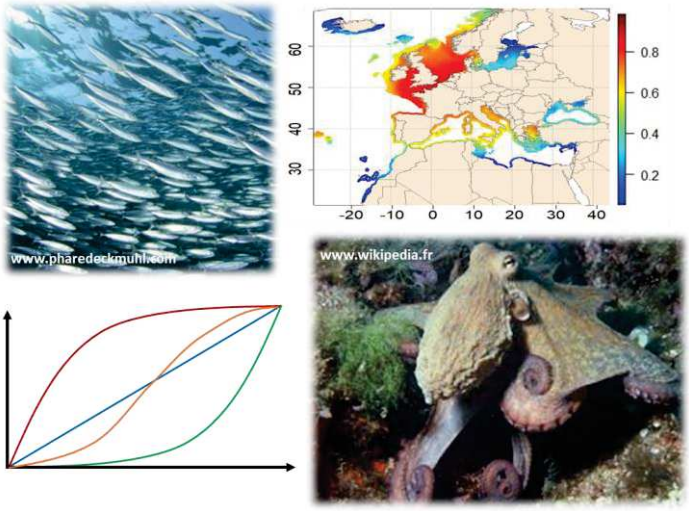
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# From species range-shifts to food-web alterations: consequences of global warming in the Mediterranean Sea

Par : Fabien BOURINET




***Soutenu à Rennes, le 11/09/2019***

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*Les analyses et les conclusions de ce travail d'étudiant n'engagent que la responsabilité de son auteur et non celle d'AGROCAMPUS OUEST*

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# List of abbreviation

LM: Linear Model

GLM: Generalised Linear Model

NLS: Nonlinear Least Square

NLRQ: Nonlinear Quantile Regression

POP: Probability of Presence

B: Biomass

ENA: Ecological Network Analysis

SPFs: Small Pelagic Fishes

TL: Trophic Level

SST: Sea Surface Temperature

F: Fishing mortality

EE: Ecotrophic Efficiency

# Résumé étendu en français

## **Contexte** :

Le réchauffement climatique impacte fortement la physique des océans. Ainsi, les courants sont modifiés, les eaux s'acidifient et se réchauffent. Ces changements de conditions environnementales impliquent des changements de distributions des espèces marines, qui ont tendances à se rapprocher des pôles, afin de rester dans des conditions environnementales qui leurs sont favorables. La température de l'eau semble être dans de nombreux cas le facteur principale déclencheur de ces mouvements, mais d'autres facteurs comme la variabilité de la température, la salinité ou la production primaire jouent aussi un rôle fort.

Le réchauffement climatique a déjà des impacts visibles, avec de nombreux déplacements observés. La température moyenne de surface va continuer d'augmenter au cours du XXI$^{ème}$ siècle. Différents scénarios, selon les choix politiques suivis, ont été initiés par le Groupement Intergouvernemental d'Etude du Climat (GIEC). Basés sur la quantification des émissions de gaz à effet de serre et aérosols, ces scénarios (Representative Concentration Pathway, RCP) couvrent différentes politiques, de la plus optimiste (RCP 2.6, +1.5°C en température moyenne à la surface du globe d'ici 2100) à la plus pessimiste (RCP 8.5, +4°C en température moyenne à la surface du globe d'ici 2100).

La Mer Méditerranée est un écosystème unique qui accueille une très grande biodiversité malgré sa relative petite taille. Elle accueille ainsi plus de 17 000 espèces, dont plus de 20% seraient endémiques. Son caractère semi-fermé conduit à des effets de « cul-de-sac » dans le contexte du réchauffement climatique, empêchant la migration des espèces vers le pôle. Enfin, elle subit une forte pression anthropique et est bordée par 23 pays différents, ce qui en fait un espace sensible mais avec une forte valeur socio-économique, avec une importante activité touristique et une activité de pêche traditionnelle.

Les changements de distribution futurs potentiels ont été étudiés pour 10 espèces à l'aide de modèles de niche écologique lors des travaux de thèse d'A. Schickele. Des cartes de distributions des espèces, qui représentent la probabilité de présence d'une espèce pour chaque cellule de la zone d'étude, ont été créés pour la décennie actuelle, et celle de 2090-2099, sous les conditions climatiques du scénario RCP 8.5.

## **Objectif** :

A partir des changements de distributions observés pour 10 espèces, l'objectif de l'étude était d'évaluer l'impact que ces changements pourraient avoir sur les écosystèmes Méditerranéen et leur réseau trophique. Plus précisément, il a d'abord été cherché une relation statistique pour passer des changements de distribution à des changements de biomasse. Cela afin de forcer des modèles Ecopath représentant le réseau trophique d'un écosystème Méditerranéen, et de suivre les conséquences de ces changements de biomasses.

## **Matériels et méthodes :**

- Relation statistique entre la probabilité de présence et la biomasse

Le travail est basé sur les cartes de distribution actuelle et future pour 10 espèces d'intérêts. Ces cartes donnent une valeur de probabilité de présence pour chaque cellule de 0.1°x0.1°.

La probabilité de présence explique l'adéquation du milieu pour l'espèce en fonction des conditions environnementales. Ces probabilités proviennent de modèles de niche écologiques, basés sur 3 paramètres environnementaux pour chaque espèce : la température de surface moyenne, sa variabilité (i.e. range annuel ou variance mensuelle), et enfin la salinité ou la production primaire.

Afin de passer des valeurs de probabilité de présence à l'abondance des espèces, j'ai cherché une relation statistique entre ces 2 paramètres. Pour cela, un jeu de donnée de biomasse spatialisée a été créé pour l'étude. La mortalité par pêche a été ajoutée quand elle était disponible, en tant que variable explicative secondaire.

Différentes modélisations ont été testées. J'ai commencé par des Modèles Linéaires (LMs) et des Modèles Linéaires Généralisés (GLMs). Puis j'ai continué avec des modèles Nonlinéaire des Moindres Carrés (NLS), avec une courbe logistique. Et enfin, j'ai réalisé des modèles Nonlinéaire de Régression Quantiles (NLRQ). Les modèles ont été comparés entre eux par une analyse des résidus et à l'aide du critère d'Akaike (AIC).

- Impact sur le réseau trophique

En utilisant la relation définie, les futures valeurs de biomasse des 10 espèces étudiées ont été calculées à partir des valeurs de probabilité de présence futures. Ces valeurs ont été intégrées dans un modèle Ecopath du Golfe du Lion. Un modèle Ecopath représente le réseau trophique, en regroupant les espèces écologiquement proches (i.e. même proies, prédateurs et habitats) dans des boites trophiques, et les relie par leurs liens trophiques. Les futures biomasses ont été appliquées sur 3 niveaux (i.e. seulement les petits poissons pélagiques ; seulement les céphalopodes ; les 10 espèces), et selon 3 méthodes de calibration (i.e. en modifiant soit la productivité des espèces, soit le régime alimentaire des prédateurs ou en laissant le logiciel adapter les biomasses des boites trophiques). Les sorties des différents modèles ont été analysées à l'aide des indices ENA à différentes échelles, afin de définir la sensibilité de l'écosystème à ces quelques changements clés induits par le réchauffement climatique

- Dynamique de la pêche combinée au réchauffement climatique

Les sorties des modèles Ecopath ont permis de paramétrer des modèles Ecotroph. Ce modèle représente l'écosystème comme un flux de biomasse à travers les niveaux trophiques. Il a permis d'étudier certains phénomènes essentiels de l'écosystème du Golfe du Lion, ainsi que l'impact de la pêche en appliquant plusieurs multiplicateurs d'efforts.

## Résultats et Discussions :

Les biomasses des petits poissons pélagiques et des céphalopodes, sous le scénario RCP 8.5, ont tendances à globalement diminuer d'ici la décennie 2090-2099. Deux stocks présentent notamment un fort effondrement (le sprat et la sardinelle), et 1 seul stock présente une augmentation importante (l'anchois). Cette diminution globalisée va probablement avoir un impact fort sur l'écosystème, en lien avec l'effet bottom-up des petits poissons pélagiques.

Les indices ENA, globalement plus faible dans le futur, montrent que l'écosystème tend à se dégrader, en perdant de la résistance et de la résilience. L'écosystème du Golfe du Lion serait plus exposé aux perturbations, internes comme externes. Il serait aussi moins complexe et moins actif. Ces changements sont induits notamment par les espèces présentant les plus forts changements de biomasse.

En analysant les sorties d'Ecotroph, l'écosystème serait actuellement exposé à une surexploitation par la pêche. Les plus forts niveaux trophiques, au-dessus de 4, sont globalement surexploités, et les stocks sont donc déjà fragilisés. D'ici 2090-2099, la diminution globale des petits poissons pélagiques risque d'impacter ces prédateurs supérieurs, en les exposant à un stress physiologique dû à un plus faible effet bottom-up. Les niveaux trophiques entre 3 et 4 ne seraient pas surexploités. Cependant, Ecotroph cache des surexploitations avérées à l'échelle de l'espèce, et parfois aggravées avec les futures biomasses plus faibles. Par leur effet bottom-up, ces espèces impactent tout le reste du réseau trophique par effet de cascade. Une régulation adaptée de la pêche semble donc essentielle pour ne pas fragiliser d'avantage l'écosystème du Golfe du Lion, dans ce contexte de réchauffement climatique.

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# I/ Introduction

Global warming is of major concern in ecology nowadays (Botkin et al., 2007; García Molinos et al., 2016). Its impacts are already visible (Millar et al., 2017; Root et al., 2003), and the expected increase in temperature (Field et al., 2014) may induce important modifications of ecosystems during the 21st century, even by limiting the global warming to the Paris Agreement target (+1.5°C above preindustrial level; Cheung et al., 2016; Masson-Delmotte et al., 2018).

Temperature is known to have important consequences on the physics of ocean including acidifications (Kroeker et al., 2013), modifications of oceanic currents (Wu et al., 2012) and sea level rising (Nicholls and Cazenave, 2010; Rahmstorf, 2007), which may affect the ecology of aquatics organisms (Beaugrand et al., 2015; Boyd and Doney, 2002; Cheung et al., 2009). Rising temperature are known to induce fish movements, which tend to get closer to the pole, in order to stay in their optimal range of temperature (Hannesson, 2007; Raybaud et al., 2017). Every species is linked to a specific ecological niche (Hutchinson, 1957). It defines the interval of values for physical and biological parameters in which the organism can grow and reproduce. For aquatics species, ocean temperature is one of the main driver of species distribution (Beaugrand et al., 2018), either the mean SST or its variability, impacting each life-stage of the marine species (Peck et al., 2013). Other factors influence the species distribution as the salinity (Bœuf and Payan, 2001) or the primary production. Species range-shifts have serious impacts on the ecosystems, modifying the local communities and food web and changing the fisheries, with consequences on local regulations and socio-economic issues (Perry et al., 2005).

Different global warming scenarios have been created, depending on the political choices. The recent RCP scenarios (Meinshausen et al., 2011; Moss et al., 2010; van Vuuren et al., 2011) are now commonly used in aquatic ecology. They are based on quantifying emissions of greenhouse gases and aerosols, combined with land use and cover. The RCP 8.5 may lead to an increase superior to 4°C by 2100 (Alexander et al., 2018).

The Mediterranean Sea is a unique ecosystem and a biodiversity hotspot (Coll et al., 2010). While this enclosed sea correspond to only 0.32% of the world's ocean volume (Bianchi and Morri, 2000), it hosts approximately 17 000 species, 20.2% of which are endemics species. This small area hosts the equivalent of 4 to 25% of the total marine biodiversity (Coll et al., 2010). Stuck between 3 continents, its character of semienclosed sea may result in a 'cul-de-sac' in the context of global warming, therefore threatening species by slowing or impeding the migration toward more suitable areas (Lasram et al., 2010). The Mediterranean Sea is also strongly threatened by multiples anthropogenic factors: the Suez Canal allows hundreds of alien species to invade the East Mediterranean Sea and compete with the local organism (Coll et al., 2010; Galil, 2007); local pollutions weaken the Mediterranean ecosystem (Whylie et al., 2003); and finally, overfishing is recurrent in this area and threatened many stocks (FAO, 2016; Tsikliras et al., 2013). Surrounded by 23 countries and suffering an important anthropic pressure, the Mediterranean Sea is a sensible place with a high socio-economic role, where take palce large touristic activities and traditional fisheries (Arkhipkin et al., 2015; Farrugio et al., 1993).

Species range-shifts have been studied by Schickele et al. (*under review*) for 7 small pelagic fishes species and 3 cephalopods species. They used 8 ecological niche models to study the physical conditions that fit the requirement of each fish. Using presence/absence data and maps of temperatures, chlorophyll concentration and salinity, they realised maps of distribution

of each species, for the current period and for future decades, to predict range-shifts. The Mediterranean Sea is a key area for this study, as an important biodiversity pool, an essential socio-economic place and an already threatened environment.

In this context of global warming, the study aimed to understand the impacts of species distribution modifications on Mediterranean food webs. More specifically, it aimed to pass from the maps of distribution to predicted future biomass and then evaluate the impact of abundance changes on a Mediterranean ecosystem (i.e. the Gulf of Lion), studying the food web modifications and the role fishing may play.

My study followed the work from A. Schickele, and is inspired by the method developed by Chaalali et al. (2016). Using the modelled species, I studied the potential statistical relationship between the outputs of ENMs and the abundance of fish. I then calculated potential biomass changes accordingly for the studied species. These values were used to force the Ecopath model of the Gulf of Lions ecosystem (Bănaru et al., 2013), to study the sensitivity of the ecosystem to a potential biomass change of important species. The outputs were analysed by the means of Ecological Network Analysis indices (ENA; Baird and Ulanowicz, 1993; Guesnet et al., 2015; Ulanowicz, 1986), defined at the ecosystem scale and the species scale. Moreover, I also used Ecotroph (Colléter et al., 2013a; Gascuel, 2005; Gascuel and Pauly, 2009) models to study the potential interactions between these changes of biomass and local fisheries.

# II/ Materials et methods

## A – Overview of the methodology

The study aimed to evaluate the implications of climate range-shifts on the food-web structure and functioning. Here, I present a synthetic overview of the three-step methodology that structured this study (**figure 1**). All methodological details are given in the corresponding sections hereafter.

First, I searched for a statistical relationship between the Probability of Presence (POP) and the Biomass (B). The POP reflects the suitability of the local environment for a species regarding environmental conditions. A spatialised B dataset has been built up to fit the relationship, based on stock assessment and Ecopath models (Christensen and Pauly, 1992; Christensen and Walters, 2004; Polovina, 1984). Different models have been tested and compared to find the optimal relationship.

In the second step, I calculated the future biomass of 10 species for 2090-2099 under the RCP 8.5 scenario, according to the relationship between B and POP. Those future biomasses were used to force 9 Ecopath models, with 3 levels of biomass application (i.e. only forcing small pelagic fishes, only forcing cephalopods and forcing all species) and 3 calibrations methods (i.e. classical Ecopath calibration, only forcing biomass, only forcing diet; details in section D.3).

In the third step I worked on the Ecopath model's outputs. I analysed the ENA indices at ecosystem and species scales, which quantified the different modifications the ecosystem went through. Then, Ecopath outputs were used to set parameters of Ecotroph models, to study the B spectrum and the impact of fishing on the ecosystem.

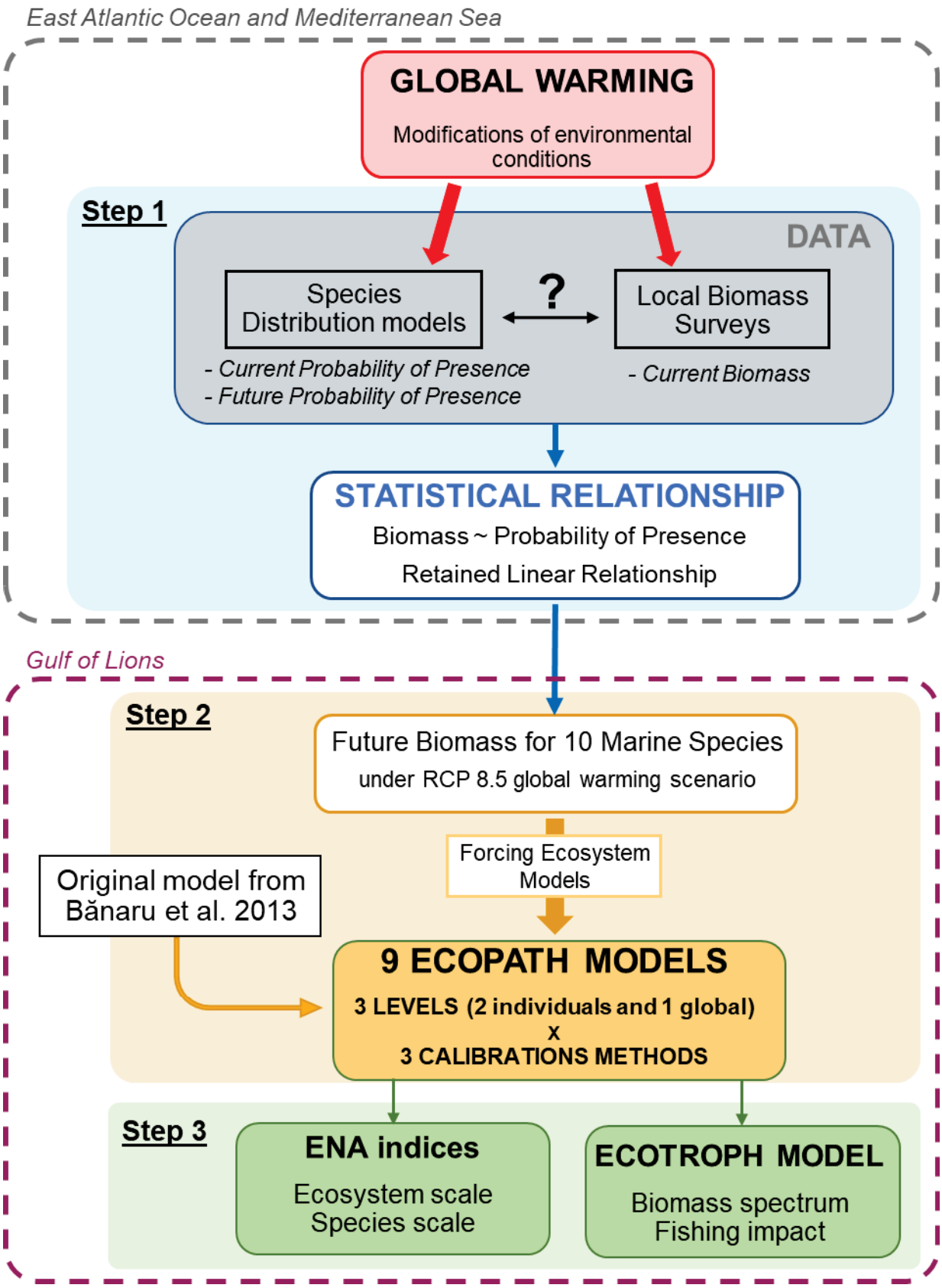



**Figure 1**: sketch diagram of the method developed during the study

## B – Study area and studied species

### 1) Studied species

My study followed the work from A. Schickele. I used the species he previously modelised and therefore worked on 10 species in total: 7 Small Pelagic Fishes (SPFs) species and 3 cephalopods species.

The 7 SPFs were: European anchovy *Engraulis encrasicolus* , the European pilchard *Sardina pilchardus,* Atlantic horse mackerel *Trachurus trachurus*, Mediterranean horse mackerel *Trachurus mediterraneus*, European sprat *Sprattus sprattus*, bogue *Boops boops* and round sardinella *Sardinella aurita*. The 3 cephalopods were common octopus *Octopus vulgaris*, common cuttlefish *Sepia officinalis* and common squid *Loligo vulgaris*.

SPFs are key organisms in the functioning of marine ecosystems. They dominate the biomass at medium Trophic Level (TL; between 3 and 3.5). They can present a top-down control on planktonic trophic levels (Cury et al., 2000) and an important bottom-up control on the top predators (Duarte and García, 2004; Frederiksen et al., 2006), directly impacting their total biomass. Therefore, SPFs are playing a central role in food webs by linking the lower trophic levels with the top predators (Cury et al., 2000). Moreover, they are an essential fishery in the Mediterranean and Black Seas representing more than 50% of the total landings of the area between 2000 and 2013 (FAO, 2016).

Cephalopods show lower values of biomass (Bănaru et al., 2013). They are sharing the TL 3.5 with the SPFs and are also a big part of the diet of some top predators (Bănaru et al., 2013). Cephalopods are important for the small scale fisheries in the Mediterranean Sea, and a traditionally socio-economical significant resource (Arkhipkin et al., 2015; Quetglas et al., 2015, 2014).

The short life-cycle of those 10 species imply important fluctuations of biomass, linked to environmental conditions (Boyle P. R. et al., 1996; Checkley et al., 2009; Doubleday et al., 2016; Peck et al., 2013), directly exposing these species to global warming, with distribution changes already observed (Peck et al., 2013; Sabatés et al., 2006).

### 2) Study area

The method developed was applied on 2 study areas, depending on the step of the study (**figure 1**). The work on the statistical relationship (step 1) was conducted for 2 SPF species for which biomass data were available. The area was defined as the Black Sea, the Mediterranean Sea and the North East Atlantic Ocean, from Mauritania to the North Sea. Every SPFs are widely distributed on the area (Schickele et al., *under review*). Ranging from warm to cold water, the area covered the optimal environmental conditions for each SPF and their range limits. The dataset then covered a wide range of POP values for each species, to establish the statistical relationship on the whole species distribution.

The ecosystem modeling work (step 2 and 3) was applied to the Gulf of Lions ecosystem, based on a previous work from Bănaru et al. (2013). The original model included all the species studied: the 7 SPFs and the 3 cephalopods.

The Gulf of Lions is an important region of the Mediterranean Sea in the context of global warming. Indeed, it is one of the 2 “cul-de-sac” regions, where the water is colder than the average Mediterranean water temperature. Therefore, the temperate-cold water species of the Mediterranean Sea may converge to this area in case of sea warming (Lasram et al., 2010).

Moreover, the plume of the Rhone River and the wide continental shelf combined with the local climatic conditions (Millot, 1990; Petrenko et al., 2005) make it one of the most productive regions of the Mediterranean Sea (Saraux et al., 2019). The area is also regularly surveyed due to the socio-economic importance of the fishery (Bourdeix and Hattab, 1985; Jadaud et al., 1994), and thereby presents many available data.

## C - Statistical relationship between probability of presence and biomass

### 1) Spatialised biomass dataset

To assess the ecological implications of species range-shifts on a Mediterranean food web, it was necessary to convert the projected changes in Probability of Presence (POP) into changes of Biomass (B). I investigated the statistical relationship between these two parameters. Temporal changes in the POP were already established in a precedent work. They used 8 ecological niches models and based on 3 environmental parameters: the Sea Surface Temperature (SST), its variability (temperature range or variability, depending of the species) and the Sea Surface Salinity (SSS) or the primary production as third variable, also depending on the species. See appendix I for more details on the original study.

To study the relationship between POP and B, a spatialised biomass dataset has been compiled for each of the 7 SPFs studied. It was primarily retrieved from 15 Stock Assessments (i) from the International Council for the Exploration of the Sea (ICES) for the Atlantic Ocean and from (ii) the Scientific, Technical and Economic Committee for Fisheries (STECF) for the Mediterranean and Black Sea. The dataset was completed by data retrieved from 22 Ecopath models available on Ecobase (Colléter et al., 2013b) which covered the study area, including the Mediterranean Sea, the Black Sea, and the North East Atlantic Ocean, from Mauritania to the North Sea. The final dataset consisted of 74 data from Ecopath models and 429 data from Stock Assessments. The data corresponded to a value of biomass, for 1 year, on a defined surface. Because SPFs were all harvested species in the Gulf of Lions, the fishing pressure may influence the fish abundance. Therefore, when available, I added the fishing mortality (F) corresponding to each biomass data into the dataset to use it as a potential variable of the statistical relationship. Despite the important data collection work, enough data for the study were found only for the European anchovy *Engraulis encrasicolus* and the European pilchard *Sardina pilchardus*.

Spatial representation of the dataset was created with QGis for both studied species, which were then rasterised under R, to obtain 1 value for each 0.1° x 0.1° cell (i.e. corresponding to the resolution of the POP data). Stock assessments covered wide areas, not corresponding to the habitat of the species (e.g. abyssal areas). Therefore, I redefined the accurate limit of the study area, according to the POP spatial coverage. The total biomass from the stock assessment was reassigned to the new accurate area.

For each geographical cell, I calculated an average biomass density, in 2 steps: as models covered several years, I first averaged the values on the time period for each model. Then, I averaged the mean values on the same area. This method avoided the bias between the different temporal coverages.

Finally, the models (i.e. one B value) covered large intervals of POP values due to their wide surface. To avoid a “plateau” effect, I average the POP for each B value.

### 2) Statistical relationship

The relationship was tested on the European anchovy and the European pilchard for which I gathered enough data. I started to calibrate Linear Models (LMs) and Generalised Linear Models (GLMs). They integrated POP, F and the interaction between these two. The best relationship was selected by analysing the p-values of the Student tests, the quality of the residuals and the Akaike Information Criterion (AIC ; Akaike, 1973) among the different fitted models.

Other models were also tested to complete the study. As an *a priori* hypothesis, I expected a logistic curve to describe the best the probability of presence – biomass relationship, with low POP values corresponding to low quality habitat, and conversely with high POP values and a potential saturation effect. This hypothesis has been tested with Nonlinear Least Squares (NLS) models, which uses the least squares method to fit a non-linear model to our set of observation. I tested this method on the 2 SPFs species with the following logistic function:

$$B \sim {}^{a}/_{(1 + \exp(-(c + d \times Pmoy))} \quad \text{(eq. 1)}$$

where *a*, *c* and *d* are constants calculated by the model, B the biomass and Pmoy the probability of presence.

The NLS model needed initialisation values for the 3 constants. *a* represent the asymptotic value of B, and was first initialised with the maximum B observed, or a value just above. None of these values allow the NLS to converge, and I had to pick lower value. The values used for the 3 constants were obtained thanks to the getInitial() function of the stats package on R, using the SSlogis Self-Starting model. It gives the 3 initial values for the logistic close to the fitted model's values, allowing the NLS to converge quickly.

The biomass data gathered for the study were in the end widely spread for the same values of POP. Therefore, I performed Nonlinear Quantile Regression (NLRQ) models on the same datasets, a method that fitted one model for each quantiles of the dataset. I obtained different curves, reflecting the values of each studied quantiles (i.e. each corresponding ecosystem type).

## D - Functional changes of the ecosystem

After investigating a potential statistical relationship between B and POP, I calculated future biomass values for the 10 studied species under the RCP 8.5 global warming scenario. These values were used to force ecosystem models of the Gulf of Lions and study the corresponding food-web modifications.

### 1) Ecopath model and food web modification

Ecopath (Christensen and Pauly, 1992; Christensen and Walters, 2004; Polovina, 1984) is a mechanistic model which represent the food web at a steady state. Organisms are grouped into trophic boxes of species with similar physiological parameters, diets and predators. Each functional group is defined by its diet (DC) and three parameters among its biomass (B), its production rate (P/B), its consumption rate (Q/B) and its unassimilated food rate (U/Q). The model is then mass-balanced, according to 2 main equations: the production (eq. 2) and the energy balance (eq. 3).

$$B_i \times (\frac{P}{B})_i = \sum_{j=1}^{N} B_j \times (\frac{Q}{B})_j \times DC_{ji} + (\frac{P}{B})_i \times B_i \times (1 - EE_i) + Y_i + E_i + BA_i \quad \text{(eq. 2)}$$

With i a trophic box of prey, and j a trophic box of one of his predators ; B the biomass ($t.km^{-2}$) ; $(\frac{P}{B})$ the production per unit of biomass ($year^{-1}$) ; $(\frac{Q}{B})$ the consumption per unit of biomass ($year^{-1}$) ; $DC_{ij}$ the percentage of i in the diet of j ; EE the ecotrophic efficiency, which is the portion of the group biomass that doesn't die of natural death (except predation), and is then predated in the ecosystems or fished ; Y the landings ($t.km^{-2}.year^{-1}$) ; E the emigration ($t.km^{-2}.year^{-1}$) ; BA the biomass accumulation ($t.km^{-2}.year^{-1}$), which can illustrate the increase or decrease of biomass of the group which isn't linked to the fishing pressure. The Eq. 2 illustrate the mechanism that all the production of a box is either predated, fished, emigrated, accumulated or eventually dead from natural mortality (other than predation).

$$Q_i = P_i + R_i + UA_i \quad \text{(eq. 3)}$$

With Q the net consumption (t); P the net production (t); R the respiration (t) and UA the unassimilated food rate (excretion essentially; t).

The model is balanced when all the boxes are at equilibrium (cf equations). If one EE value is superior to 1, the model is unbalanced. In that case, the parameters are modified following a trial and error procedure, starting by the most uncertain ones: first, the diet of the predators, decreasing the predation pressure on the unfitted prey box; then the P/B values can be increased; finally, the Q/B of the predators may be decreased. The EE represents the proportion of organism which do not die from natural death (predation excluded). This value must not be superior or equal to 1. A threshold value of 0.95 has been applied during the study for every box. When the model was balanced, I obtained an illustration of a food web at steady state, for the studied period.

### 2) Application to the Gulf of Lions

I used the Ecopath model from Bănaru et al. (2013) (**figure 2**) which represented the ecosystem of the Gulf of Lions for the period 2000-2009, covering depth between 0m and 2500m. It consisted of 40 functional groups, with 5 groups of primary producers (phytoplankton, phytobenthos, posidonia and macrophyte), 12 groups of invertebrates, 18 groups of fish, 1 group of seabirds and 2 groups of cetaceans.

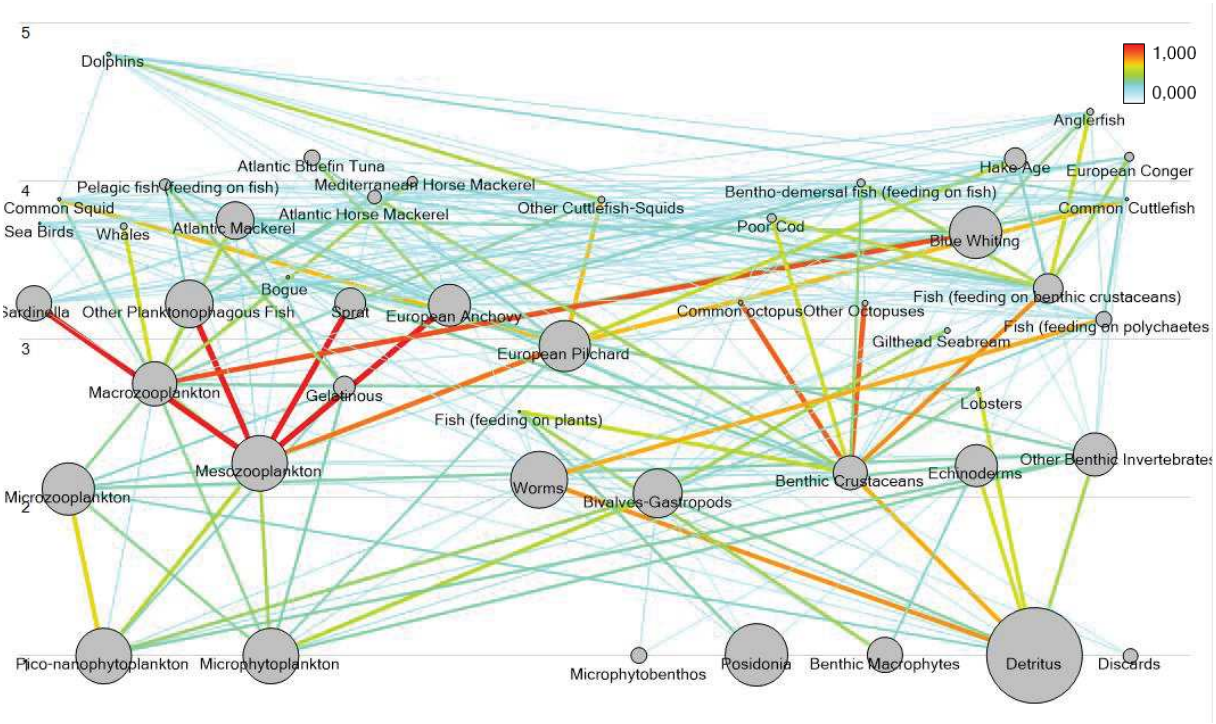



**Figure 2** : food-web of the model adapted from Bănaru et al. (2013). Circles are the trophic boxes, linked with trophic interactions (predation/ontogeny). Colors represent the intensity of the flow.

The present study aimed to evaluate the implications of climate-induced range shifts of several marine species on the whole ecosystem of the Gulf of Lions. For this study, I isolated each studied species in a unique box, to assess precisely the effect of each species modifications on the food web. The new boxes were created according to the data of the original publication of Bănaru et al. (2013) when available. Else, the missing data were retrieved from scientific publications (see details below) on the study area, or similar Ecopath models.

For the SPFs, the B were retrieved from the original publication. The other parameters had to be determined.

For the European sprat, the P/B was obtained from the literature (Avsar, 1995) while the Q/B was calculated (eq. 4), using a relationship in Christensen (2005) :

$$\log\left(\frac{Q}{B}\right) = 5.847 + 0.280 \times \log(Z) - 0.152 \times \log\left(W_{infini}\right) - 1.360 \times T' + 0.062 \times A + 0.510 \times h + 0.390 \times d \quad \text{(eq. 4)}$$

With Z the total mortality : at steady state, Z = (P/B) (Allen, 1971) ; $W_{infini}$ the asymptotic maximum weight of the species ; T' = 1000 x Temperature (K) ; A the aspect ratio of the caudal fin and h and d which are binary variables (h = 1 if the organism is herbivore, 0 else ; d = 1 if the organism is detritivore, 0 else) that define if the species is a predator, an herbivore or a detritivore. The value of A was taken from FishBase (Froese and Pauly, 2019).

For the round sardinella, the P/B and Q/B were retrieved from the Ecopath model of the Gulf of Gabès (Hattab et al., 2013).

For both the round sardinella and the European sprat, originating from the group “other planktonophagous fish”, we estimated that the landings were proportional to the distribution of biomass into the original group. Finally, the diet was kept the same as the original box’s one.

For the bogue, the P/B was found in the literature (Allam, 2003; Monteiro et al., 2006) while the Q/B was taken from the Gulf of Gabès Ecopath model (Hattab et al., 2013). Bogue was aggregated with *Sarpa salpa* which is a shore species feeding mainly on Posidonia, not targeted by fishermen. Then, we hypothesised that bogue supported 100% of the landings of the group.

When individualizing the SPFs, it has been first decided to keep the same diet as the original group. The bogue, previously aggregated with *Sarpa salpa*, presented an excessive herbivory diet with a TL = 2.5. I defined a new specific diet based on the information I found in the literature (Derbal and Kara, 2008; El-Maremie and El-Mor, 2015; Froese and Pauly, 2019; Valls et al., 2012).

The value of unassimilated consumption was the same from the original box.

The same work has been made for the 3 species of cephalopods, but with less data available. The biomass of the different octopuses were retrieved from trawl surveys in the Gulf of Lions between 1983 and 2009 (Farrugio, 2013). The landings were proportional to the biomass proportions, as not accurate data was available. For the squids and the cuttlefish, no data was found in the Gulf of Lions. The percentage has been deduced from Silva et al. (2011). The landings were defined based on the few information I could find (Arkhipkin et al., 2015; Sánchez and Martín, 1993).

Because the cephalopods encountered in the model are semelparous, they have high natural mortality (Anderson et al., 2002; Boyle and Rodhouse, 2005). To reflect it, I defined specific lower threshold values of EE for the cephalopods. Thus, EE had to be inferior to 0.9 for cuttlefishes and squids, and inferior to 0.85 for octopuses (while it had to be inferior to 0.95 for the other boxes). The EE in the original model from Bănaru et al. (2013) were above the defined threshold. Then I increased the P/B by 10% for octopuses compared to the original values. For the common cuttlefish and the common squids (which exposed lower B values after the individualisation), I increased the P/B based on the equation of Allen (1971) : $P/B = Z = M + F$. M was supposed to be constant between the species, but the F (ratio of landings over the B) increase when B decrease. Finally, to reach EE = 0.9, the P/B were slightly increased.

### 3) Forcing of Ecopath model with future biomass data

By applying these modifications, I built my baseline models of the current situation in the Gulf of Lions. The future biomasses were calculated for the 10 studied species for the 2090-2099 period under the RCP 8.5 scenario using the selected relationship. The future B were integrated progressively, in 3 levels: (i) by forcing only the SPFs, (ii) by forcing only the cephalopods and (iii) by forcing all the studied species, to look for potential synergic effects.

Because these changes unbalanced the model, a calibration was conducted consequently, equilibrating the B, P/B, and diets until the EE values of every species reached the threshold value. To assess the sensitivity of future Ecopath models to calibration hypotheses, I applied 3 calibration methods: (i) a “classical” Ecopath calibration, modifying the diet of predators and the P/B of the prey, with fixed percentages, (ii) fixing the EE values, and leaving Ecopath calculate the new biomass to fit the model and (iii) modifying the predators diet proportionally to the biomass changes. At the end, I calibrated 9 new models, 3 calibrations methods for each of the 3 levels. The second calibrations method impacted every trophic boxes of the model, while the 2 others only modified the values of the boxes directly unbalancing the model (studied species and major predators).

### 4) Food web descriptors

The present and future Ecopath models were compared using different indices to assess the relative importance of indirect effects of species range shifts in the Gulf of Lions ecosystem and more generally, to evaluate how relationships among organisms may be altered by climate change. Therefore, I established two sets of indices based on Ecological Network Analysis (ENA; Baird and Ulanowicz, 1993; Guesnet et al., 2015; Ulanowicz, 1986) indices. The first one characterised the functions of the ecosystem and more specifically the food web. Most of them were already integrated in the EwE software (Christensen et al., 2005). The second set of indices derived several ENA indices to the species level to evaluate the participation of each species to the global ENA indices. The indices used are resumed in Table 1.

Table 1: List of the indices used to compare current and future Gulf of Lions ecosystem

| Indices | Definition | Equation |
|---|---|---|
| Total System Throughput TST (Ulanowicz, 1986) | Sum of all the flows in the ecosystem | TST = consumption + export + respiration + flows to detritus<br>$TST = \sum_{i=1,j=1}^{n} T_{ij}$ ; $T_{ij}$ energy flow from j to i |
| Ascendency A (Christensen et al., 2005; Ulanowicz, 1992) | Measure of the complexity and activity of the ecosystem | A = TST x I where<br>$I = \sum_{i=1,j=1}^{n} f_{ij} \times Q_i \times \log\left(f_{ij} / \sum_{k=1}^{n} f_{kj} \times Q_k\right)$<br>$f_{ij} = T_{ij} / \sum_{k=1}^{n} T_{kj}$ ; $Q_i = \sum_{k=1}^{n} T_{ki} / \sum_{l=1,m=1}^{n} T_{lm}$ |
| Capacity C (Christensen et al., 2005; Ulanowicz, 1992) | Theorical maximum values of the ascendency | C = H x TST where<br>$H = \sum_{i=1}^{n} Q_i \times \log(Q_i)$ |
| Overhead O (Ulanowicz, 1986) | Measure the potential of increase of the ascendency, the unorganised part of the system | O = C - A |
| Connectance $C_i$ (Christensen et al., 2005) | Ratio between the number of realised links between boxes and the maximum number of possible links | $C_i = N / (N-1)^2$<br>Where N is the number of box |
| Relative ascendency A/C (Guesnet et al., 2015; Ulanowicz, 1986) | Part of the ascendency in the capacity of the ecosystem. Fraction organised in the system | $\frac{A}{C}$ |
| Average Path Length APL (Christensen et al., 2005; Finn, 1980) | Average number of boxes through which a unit of C passes from the inflow to the outflow | $APL = TST / (\sum Export + \sum Respiration)$ |
| Finn's Cycling Index FCI (Finn, 1980) | Fraction of the flow which is recycled in the ecosystem | $FCI = T_c / TST$ with $T_c$ the biomass recycled. |

| | | |
|---|---|---|
| System Omnivory Index SOI (Libralato, 2008) | Mean Omnivory Index of each box, weighted by the logarithm of the consumer's food intake The OI is the variance of the TL of every boxes consumed by the predator | $SOI = \frac{\sum_{i=1}^{n}(OI_i \times \log(Q_i))}{\sum_{i=1}^{n}\log(Q_i)}$ |
| Mean Trophic Level of catch MTL (Pauly et al., 1998) | Weighted mean of the trophic level of the landings | $MTL = \frac{\sum_{i=1}^{n} TL_i \times Landings_i}{\sum_{i=1}^{n} Landings_i}$ |
| Total Catch TC | Sum of the different landings | |
| Keystoness KS1 (Libralato et al., 2006), KS2 (Power et al., 1996) and KS3 (Valls et al., 2015) | Values that quantifies the role of the species/box in the ecosystems, based on their biomass and their trophic impacts | $KS1 = \log[(\varepsilon_i \times (1 - p_i)]$ <br> $KS2 = {\varepsilon_i}/{p_i}$ <br> $KS3 = \varepsilon_i \times drank(B_i)$ <br> Where $\varepsilon_i = \sqrt{\sum_{j \neq i}^{n} m_{ij}^2}$ ; $p_i = \frac{B_i}{\sum_{k=1}^{n} B_k}$ ; drank design the descending rank. |
| Relative Trophic Impact (Ulanowicz and Puccia, 1990) | Impact of the species in the food-web, relative to the maximum value in the ecosystem | $RTI_i = {\sqrt{\sum_{i \neq j}^{n} MTI_{i,j}^2}}/{Max(MTI)}$ <br> $MTI_{i,j} = DC_{i,j} - FC_{i,j}$ ; $DC_{ij}$ is the diet composition term; $FC_{ij}$ is the proportion of predation on j due to i |

### 5) Ecotroph model and impact of fishing

Because fishing pressure is a major factor impacting fish biomass, I studied the combined effect of fishing pressure and global warming using the Ecotroph model.

Ecotroph (Colléter et al., 2013a; Gascuel, 2005; Gascuel and Pauly, 2009) represents the ecosystem as a continuous biomass spectrum distributed along the TL. It is a simplified representation of the ecosystem that dispence the notion of species, to study the whole ecosystem functioning and dynamics. It is based on the biomass flowing through the food web: a particle of carbon enters at TL = 1 (*i.e.* primary producer) and progress along the TLs thanks to ontogeny and predation (**figure 3**). All the particles together constitutes the flow, defines by its speed $K_\tau$ (in TL.year$^{-1}$) (eq. 5) and its intensity $\Phi_\tau$ (t.year$^{-1}$) (eq. 6). These two equations are used to calculate the biomass at each trophic level (eq. 7).

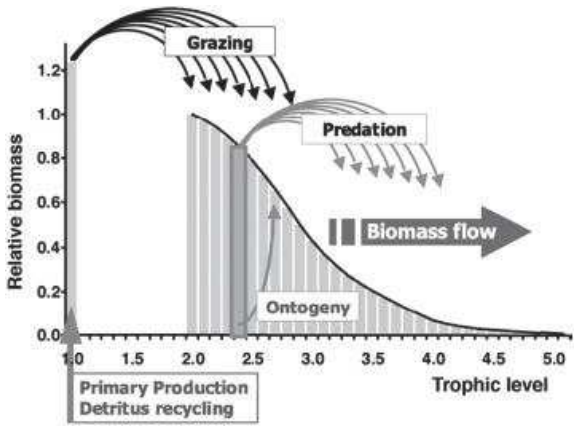



**Figure 3** : Theoretical illustration of the biomass flow in Ecotroph (Gascuel and Pauly, 2009).

$$K_\tau = \left[K_{cur,\tau} - F_{cur,\tau}\right] \times \left[1 + \alpha_\tau \times \frac{B_{pred}^{\gamma} - B_{pred,cur}^{\gamma}}{B_{pred,cur}^{\gamma}}\right] + F_\tau \quad \text{(eq. 5)}$$

With $F_\tau$ the fishing mortality at TL = $\tau$ ; $B_{pred}$ the predator biomass of trophic groups from TL = $\tau + 1$ ; $K_{cur,\tau}$ , $F_{cur,\tau}$ and $B_{pred,cur}$ applied for the current situation ; $\alpha_\tau$ is the natural mortality rate (dependent of the abundance of predators) ; $\gamma$ the shape parameter defining the top-down relationship.

$$\Phi_{(\tau+\Delta_\tau)} = \Phi_\tau \times \exp[-(\mu_\tau + \varphi_\tau) \times \Delta_\tau] \quad \text{(eq. 6)}$$

With $\mu_\tau$ the net natural loss rate of biomass flow ; $\varphi_\tau$ the rate of fishing loss

Finally, the biomass at each TL is calculated by:

$$B_\tau = \frac{\Phi_\tau}{K_\tau} \times \Delta_\tau \quad \text{(eq. 7)}$$

By considering the fishing pressure, I applied different values of fishing effort multipliers (mE) and studied their effects in a single simulation. The case mE = 0 simulated the unexploited ecosystem (Colléter et al., 2013a).

The Ecotroph models were parametrised using the outputs of the Ecopath models balanced previously (**Figure 1** – step 2). Ecotroph use as inputs the values of B, P/B and landings and the TL (calculated by the EwE software). In addition, the accessibility of each fished species is integrated to Ecotroph. The accessibility defines the part of the biomass that would be fished if we could apply an infinite fishing pressure. It depended of the species, the biotope and the fishing technique and can not be equal to 1. Characteristics of the species, the fishing gear and the area can decrease the accessibility value, impeding to access to the full stock (e.g. rocky ground, deep canyons or wide stocks). Because accessibility values were not available from the Gulf of Lions, they were defined according to expert knowledge.

To thoroughly analyse the fishery, the landings have been separated in 3 fleets respectively corresponding to: the fleet 1 for the 7 SPFs, the fleet 2 for the 3 cephalopods species and the fleet 3 for the remainders. To simplify the interpretations, I worked under the hypothesis of constant landings through time.

# III/ Results

## A – Biomass – Probability of Presence relationship

The statistical relationship has been tested for only 2 species: the European anchovy and the European pilchard because of data availability. Here I present the results for the European anchovy as an example while the results for European pilchard are presented in Appendix II.

Regarding the high p-values (> 0.05) and the residual analysis, LM are not considered as appropriate models to investigate the statistical relationship (Appendix III). GLMs show similar results. Most of the models present decreasing curves, not matching the theory: higher POP values reflects highly favorable environmental conditions for the species, leading to higher abundance of the local stock (Chaalali et al., 2016; based on the ecological niche theory from Hutchinson, 1957). Based on the p-values and the AIC, the best GLM correspond to the inverse Gaussian error distribution and the identity link function (**figure 4a**). The residual analysis (**figure 4b, c, d and e**) shows that GLM's hypothesis are not followed: the residuals are not homogeneously and randomly spread (**figure 4b and d**) along the fitted values. According to the QQ plot, they are not normally distributed neither (**figure 4c**). One point may

be considered as an outlier (**figure 4e**, point 1), but does significantly influences the model. Therefore, we decided not to keep this relationship.

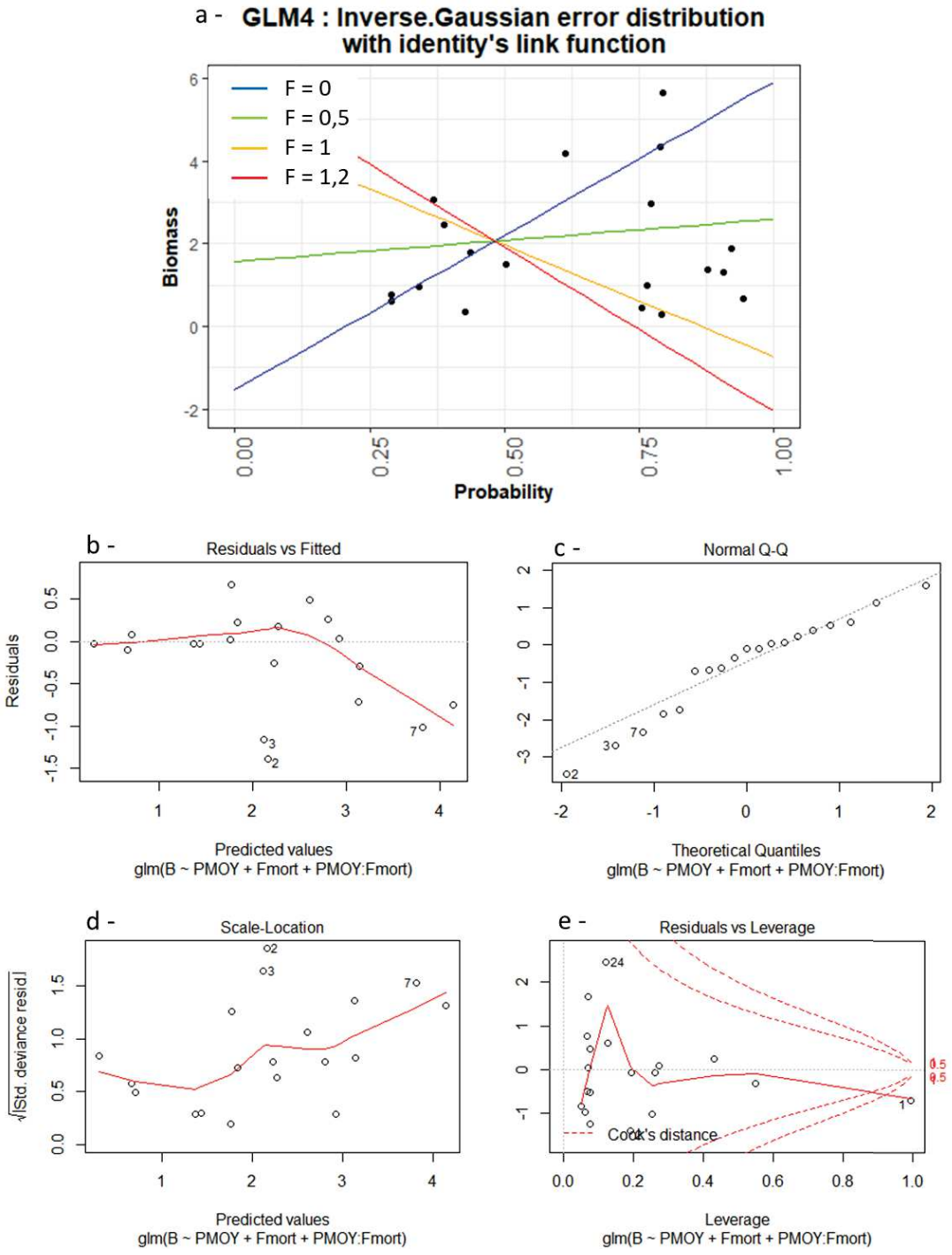



**Figure 4**: Analysis of the best GLM: (a) GLM model; (b), (c), (d) and (e) are the residual analysis plots

The same observations are made for the NLS. The data are not distributed along a logistic curve as expected but are rather widely distributed. Data are also missing at low POP which may hinder model quality. This distribution pattern leads to 2 “plateaux” at the start and the 2nd half of the POP values (**figure 5a**). It explains the unusual pattern in **figure 5c**: most of the

POP values are fitted to the same B value. The residuals are not homogeneously spread and are not normally distributed (**figure 5d**). The relationship is not kept.

The last model tested is NLRQ which showed interesting results (**figure 5b**). The curves divide themselves among the data, however more data are needed to accurately fit NLRQ models. Indeed, with only 19 points for the European anchovy and by cutting it in basic quantiles (25, 50, 75 and 90), the relationships were only fitted on 2 to 5 points. With few points, residual analysis was not significant.

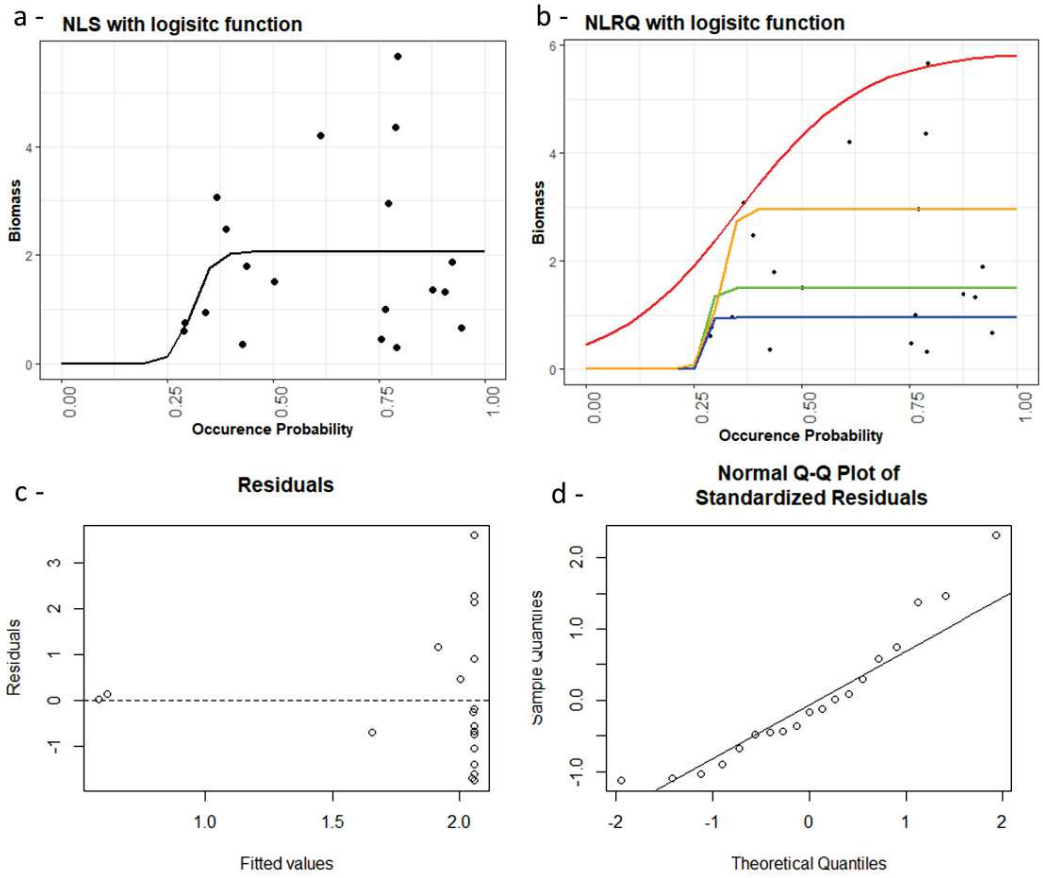



**Figure 5**: plot of the (a) NLS plot, (b) NLRQ plot and (c), (d) the residual analysis for the NLS

Because the data were insufficient to fit a satisfying statistical relationship between the B and the POP, I decided to make the same hypothesis as Chaalali et al. (2016). Therefore, I considered an increasing linear relationship between the B and the POP (eq. 8) to calculate the future biomass for the 10 species:

$$B_{futur} = \frac{B_{current} \times POP_{futur}}{POP_{current}} \quad \text{(eq. 8)}$$

## B – Biomass changes and impacts on the food web

### 1) Adaptation of the model

The original model from Bănaru et al. (2013) was adapted for the purpose of this study, isolating the studied species in unique boxes, to evaluate the impact of their range-shift. I

defined new specific values for the box parameters, retrieved from Ecopath models or publications on the Gulf of Lions or similar area. New parameters are resumed in Table 2. The diet for the bogue is given in appendix IV.

Table 2: inputs values used for the new individualised boxes of the Ecopath model of the Gulf of Lion

| Parameter | Value | References |
|---|---|---|
| Round sardinella | | |
| Biomass | 1.204 | (Bănaru et al., 2013) |
| P/B | 0.853 | (Hattab et al., 2013) |
| Q/B | 9.635 | (Hattab et al., 2013) |
| Landings | 0.0014 | Estimated |
| European sprat | | |
| Biomass | 0.860 | (Bănaru et al., 2013) |
| P/B | 1.64 | (Avsar, 1995) |
| Q/B | 2.650 | Calculated |
| Landings | 0.001 | Estimated |
| Bogue | | |
| Biomass | 0.1 | (Bănaru et al., 2013) |
| P/B | 1.161 | (Allam, 2003; Monteiro et al., 2006) |
| Q/B | 19.81 | (Hattab et al., 2013) |
| Landings | 0.1 | Estimated |
| Common octopus | | |
| Biomass | 0.0144 | (Farrugio, 2013) |
| P/B | 3.3 | Increased from Bănaru et al. (2013) |
| Q/B | 8.5 | (Bănaru et al., 2013) |
| Landings | 0.0360 | Estimated |
| Common cuttlefish | | |
| Biomass | 0.0133 | (Silva et al., 2011) |
| P/B | 3.823 | Calculated ; (Allen, 1971; Bănaru et al., 2013) |
| Q/B | 9.1 | (Bănaru et al., 2013) |
| Landings | 0.00720 | (Arkhipkin et al., 2015; Sánchez and Martín, 1993) |
| Common squid | | |
| Biomass | 0.00778 | (Silva et al., 2011) |
| P/B | 4.001 | Calculated ; (Allen, 1971; Bănaru et al., 2013) |
| Q/B | 9.1 | (Bănaru et al., 2013) |
| Landings | 0.00520 | (Arkhipkin et al., 2015; Sánchez and Martín, 1993) |

### 2) Calculated future biomass

Using the mean future POP on the study area, I deduced the future biomass with the Eq. 8. The percentages compared to the original values for the 10 species are presented in **figure 6**.

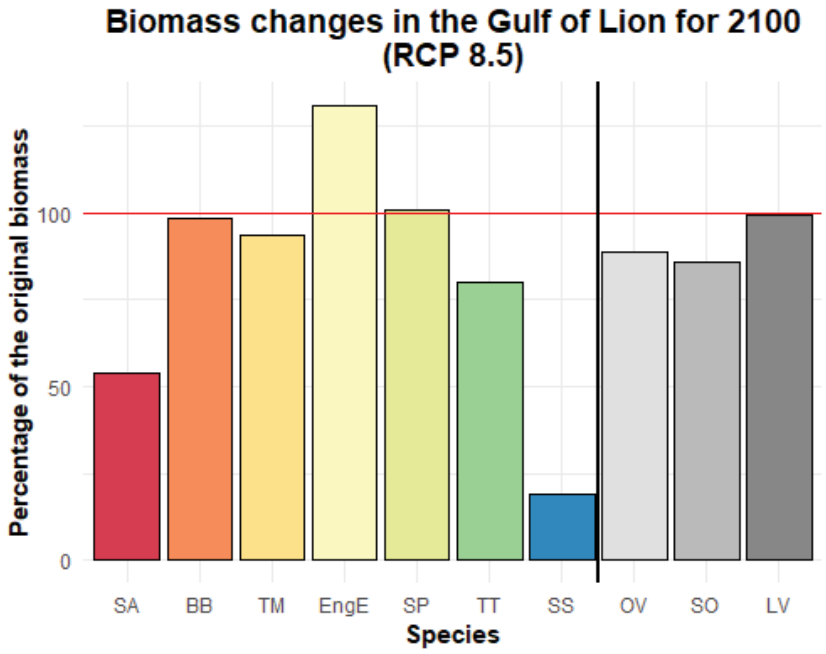



**Figure 6**: Percentage of the original value of biomass for the 10 species. SA = round sardinella; BB = bogue; TM = Mediterranean horse mackerel; EngE = European anchovy; SP = European pilchard; TT = Atlantic horse mackerel; SS = European sprat; OV = common octopus; SO = common cuttlefish; LV = common squid.

The round sardinella, the bogue, the Mediterranean horse mackerel, the Atlantic horse mackerel and the European sprat show lower future biomass value, conversely to the European pilchard and the European anchovy. The European sprat see a potential collapse of its biomass, with a decrease of 81.1% by 2090-2099. On the contrary, the European anchovy presents a potential biomass increase of more than 30%. This increase may have strong biological and economical impacts in the future because of this species' importance in terms of fisheries and essential role in ecosystem (Bănaru et al., 2013).

The 3 species of cephalopods present lower potential future biomass. The main changes are observed for the common cuttlefish and the common octopus.

### 3) Calibrations and indices evolutions

Here I present the percentages of differences for the ENA indices between 2000-2009 and 2090-2099 under RCP 8.5 for the 9 models (i.e. 3 levels and 3 calibrations). The ecosystem scale indices are presented in **figure 7**, the species scale indices in **figure 8**. Some indices are not represented as they do not add any information (e.g. the Overhead that follows the tendencies of Ascendency and Capacity).

Total biomass changes never exceed 2.82% of the total biomass in the ecosystem (in absolute values; Detritus and Discards not included), resulting in 0.89% of total biomass changes (when accounting both increases and decreases).

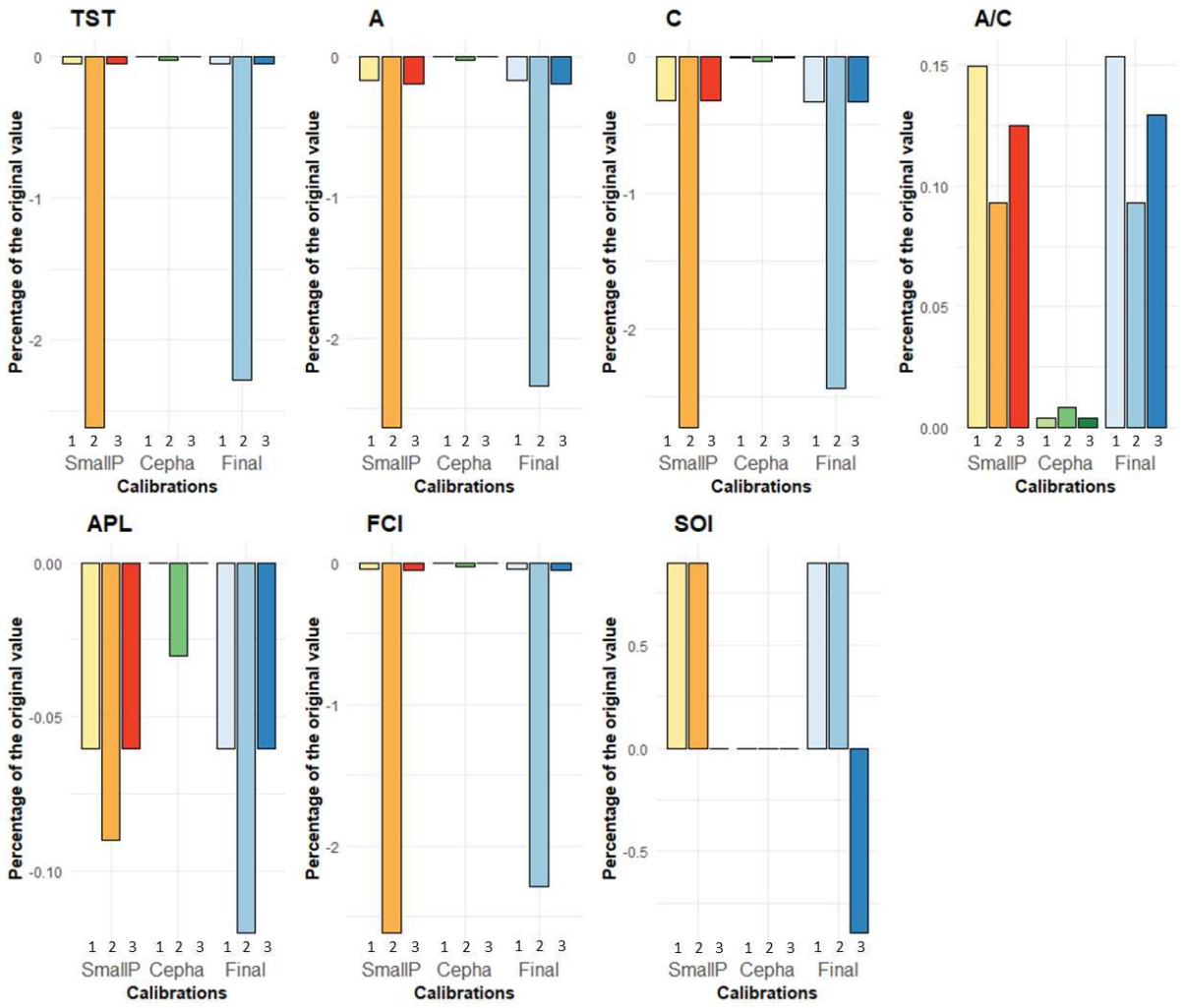



**Figure 7**: percentage of the original biomass for the first set of indices for each calibration methods, numbered as follows: 1 for the classical one, 2 for the fixed EE and 3 for the diets proportional to the biomass changes. The 3 levels are designed as SmallP when applying only the SPFs future biomass; Cepha when applying only the cephalopods future biomass; and Final for the global one.

Regarding **Figure 7**, TST, A, C, APL and FCI present similar global tendancies, with lower future values (negative percentages) for every calibrations. On the contrary, the A/C ratio increase for every cases. SOI show a different pattern: higher future values the 2 first calibrations on the first and last levels, and lower future value for the last calibration method on the final level. SOI evolve with the same difference value every time: +/- 0.002, which lead to the same fixed percentage value (+/- 0.85%).

For all the indices, the second levels (i.e. applying only the future cephalopods biomass) presents the lowest evolutions.

From the calibration point of view, the first and second method show very closed values. The second calibration presents importantly differents percentages values: more negative percentages for TST, A, C, APL and FCI; and less positive for the A/C (except on the second level).

Except for the second calibration on TST, A, C and FCI, the global changes do not exceed the global biomass changes (0.89%).

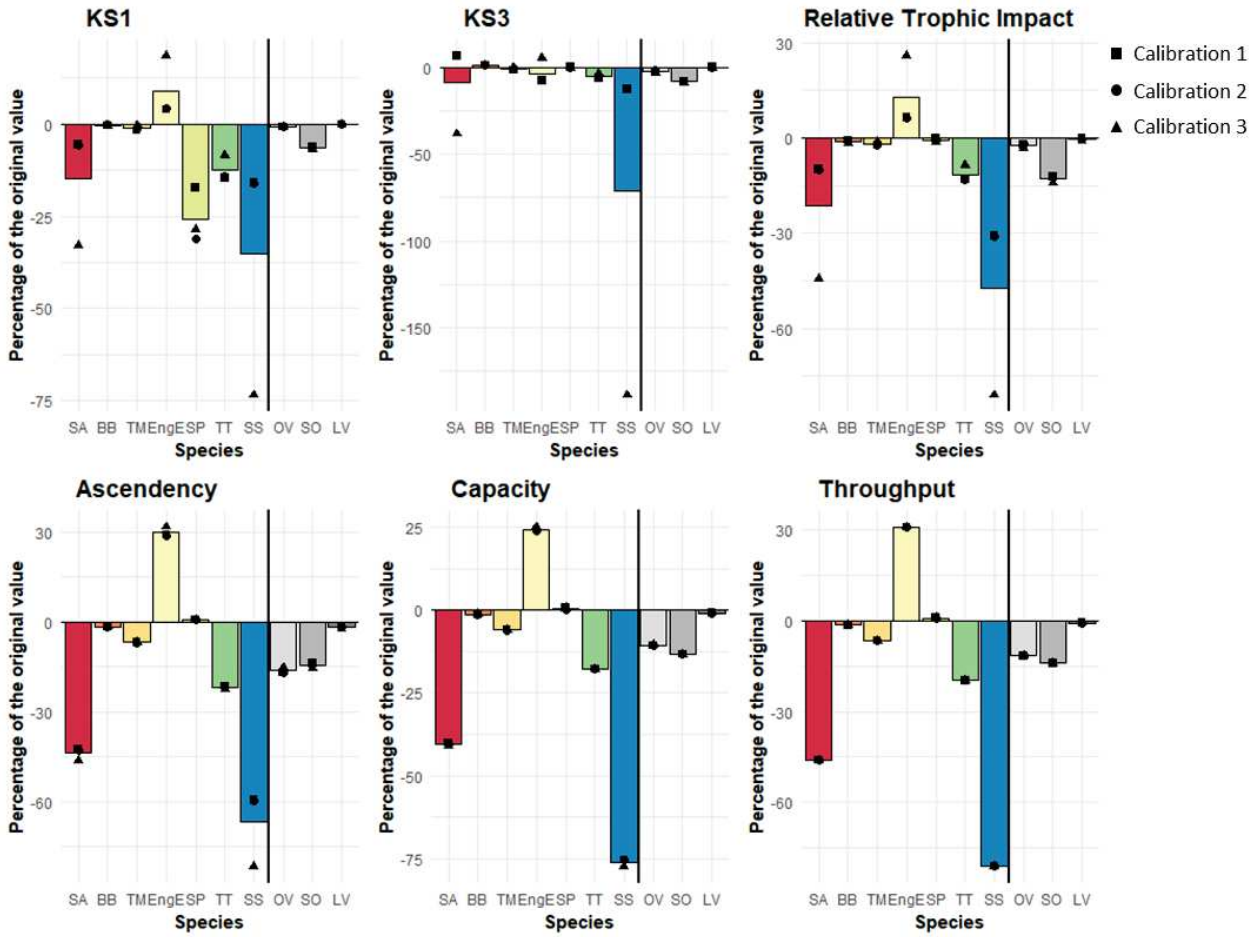



**Figure 8**: percentage of the original biomass for the second set of indices for each calibrations of the final level. Bars correspond to the mean percentages between the 3 calibrations. Species codes: SA = round sardinella; BB = bogue; TM = Mediterranean horse mackerel; EngE = European anchovy; SP = European pilchard; TT = Atlantic horse mackerel; SS = European sprat; OV = common octopus; SO = common cuttlefish; LV = common squid.

**Figure 8** presents the percentages of differences for the second set of indices only for the final level (i.e changing the biomass values for the 10 species). The results for the first and second level are presented in appendix V.

Throughput (T), A, C and RTI show similar tendencies, looking close to the biomass changes: the European sprat show the strongest differences, as it is exposed to the strongest diminution of biomass in the future. The common cuttlefish has a slightly lower decrease in B than the common octopus, but show a more important decrease in C, T and RTI than him.

KS indices present slightly different pattern, linked with the nature of their respective equations. KS3 show mostly negative mean percentages, while KS1 show a positive evolution only for the European anchovy. KS indices show similar variations as the B variations. KS1 and KS3 are then first drove by the trophic impact, which follow the B variations. The common

octopus, even though having a B decrease by more than 11%, barely see its RTI, KS1 and KS3 move.

Few differences can be observed between the calibration's methods for the Ascendency, Capacity and Throughput. KS1, KS3 and Relative Trophic Impact are more sensitive to the calibration method, with more extreme evolutions on the third calibrations for the European sprat, the round sardinella and the European anchovy.

On the species level, the European sprat and the round sardinella show the largest negative evolutions, whatever the index is. On the contrary, the European anchovy shows the only important positive evolution, except for the KS3. Cephalopods present negative percentages for every index.

The 2nd most important changes for the KS1 index is from the European pilchard, while its biomass and trophic impact slightly change. In fact, the KS1 values for this species are very low, close to 0. The results presented are percentages of evolution. A very low evolution on a very low value can lead to high percentage change. For example, the KS1 of the European pilchard goes from 0.00960 in the baseline model to 0.00686 in the Final 3 (third level, third calibration method), which lead to 28.5% differences, even though the absolute difference is very small.

## C – Flow analysis and impact of fishing combined to the global warming

Ecotroph represent the ecosystem as a biomass spectrum through the TL. The two spectrums are presented in **figure 9**, for the initial Ecopath model (**figure 9a**) and for the final model (third level, calibration 1; **figure 9b**). The spectrum shows the structure of the ecosystem, dominated first by the zooplankton (TL between 2 and 2.4]), and then by the SPFs around TL 3 (SPFs are the colored part of the spectrum). The biomass decreases at higher TL, with small abundances of top predators.

The spectrum spreads the B along the TL, making low B values not visible on the spectrum. However, some changes are still noticeable: the difference between **Figure 9a** and **Figure 9b** shows the quasi-disappearance of the European sprat in blue with the strong diminution of the round sardinella in red and the increase of the European anchovy in yellow for 2090-2099 (**figure 9b**). The top of the curve at TL 3.1 is slightly eroded in **figure 9b**, showing the global biomass diminution of the SPFs.

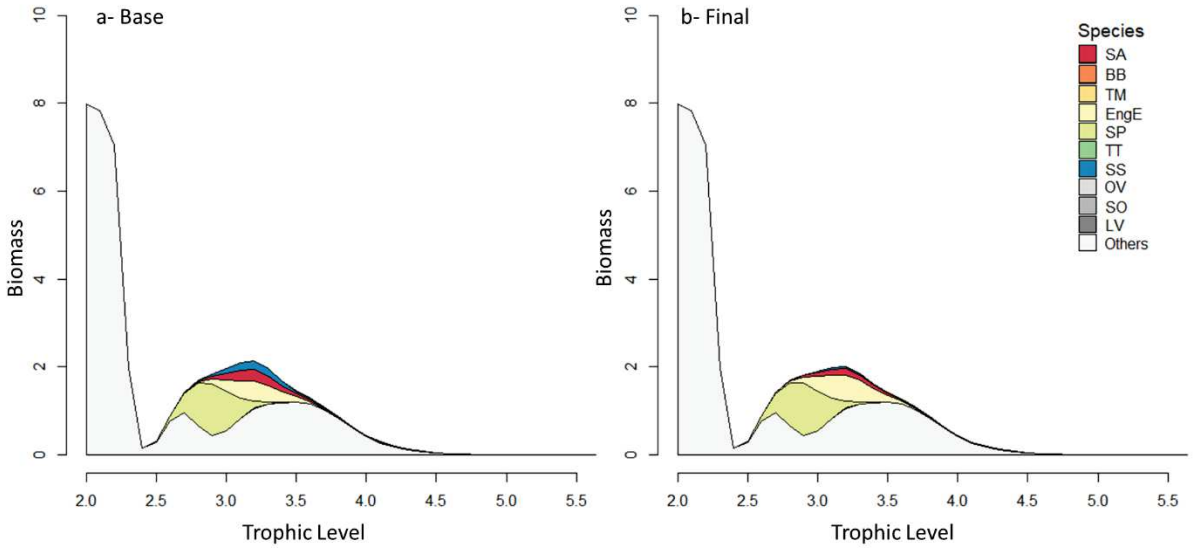



**Figure 9**: biomass spectrum for (a) the initial Ecotroph model and (b) the third level-first calibration Ecotroph model

The accessibility values used in the Ecotroph models are presented in Appendix VI. They have been deduced from expert knowledge, based on the specificity of the area, the fishing gear and the species.

I started the study with lower values of accessibility for the hake, the European conger and the anglerfish. It led to an unrealistic overexploitation and an impossible Ecotroph model. After expert consultations, the values were increased to a more realistic situation.

The sensitivity analysis of the accessibility values shows a low sensibility for this parameter. I obtained was on the total catches under the biggest fishing pressure. It reaches ± 4.86% of differences at TL = 2.9 and does not exceed +/-1% most of the time. The graphic is presented in Appendix VII.

Ecotroph studies the ecosystem under different fishing efforts multipliers (mE) (**Figure 10**). Theoretically, the more we fish, the less fish stay in the ecosystem. The TL 2 is fished only for a few echinoderms and bivalves, which represent only small part of this TL. This explains the small sensibility to mE values, most of these organisms are not fished. **Figure 10a** shows that TL between 3 and 3.5 have the most important B variation along the mE, linked with their high biomass and the important fisheries of European pilchard and European anchovy. Top predators (TL superior to 4) have very low B values with high fishing pressure, showing a high sensibility toward high fishing pressure.

At the TL between 3 and 3.5, mainly represented by the studied species, the landings are positively correlated to the mE. But with smaller intervals increase in catch at high mE, it shows that it reaches the upper limits of landings rise, and further augmentation may lead to overexploitation. Conversely at high TL, superior to 4, the curves under high mE produce less catches than the one with medium mE. The limit is reached, and high mE lead to an overexploitation of these TL.

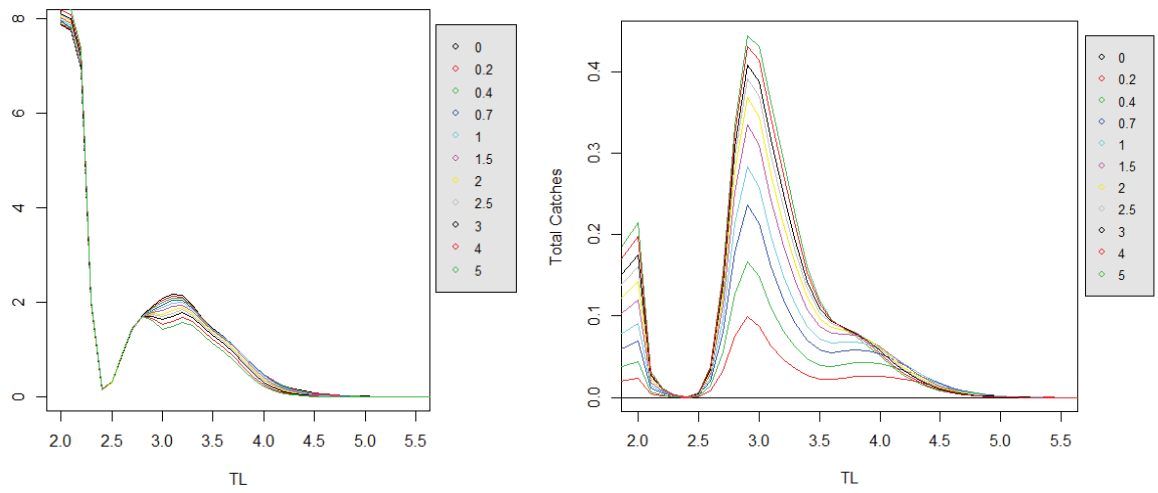



**Figure 10**: biomass spectrum (a) and total catches spectrum (b) from the Ecotroph model with different fishing effort multipliers

Ecotroph calculate the $E_{0.1}$ for each TL (**figure 11**). $E_{0.1}$ is considered a good proxy for the $E_{MSY}$ (Deriso, 1987). Comparing to 1 (the current fishing pressure) the value given by Ecotroph brings an interesting indication for the actual exploitation: over 1, the fishing pressure can be increased to reach the MSY; under 1, it is already overexploited (compared to the MSY) and fishing pressure must be decreased. Here also, every species of the ecosystem is considered, the fished and non-fished ones. This biases the actual fishing pressure, overestimating the resilience of the ecosystem. This phenomenon is aggravated at low TL and get closer to the accurate situation at high TL. Still, it shows that high TL are already overexploited and weakened. The TL between 3 and 4 are underexploited on the graphics. But some organisms are not fished (or with very low F) and must not be in the future. The global under exploitation hides differents pressures of exploitations at the species levels, with some unfished species, and some more heavily fished. The common octopus for example is strongly overexploited, exaggerated with its future biomass changes (F = 2.8 in 2090/2099).

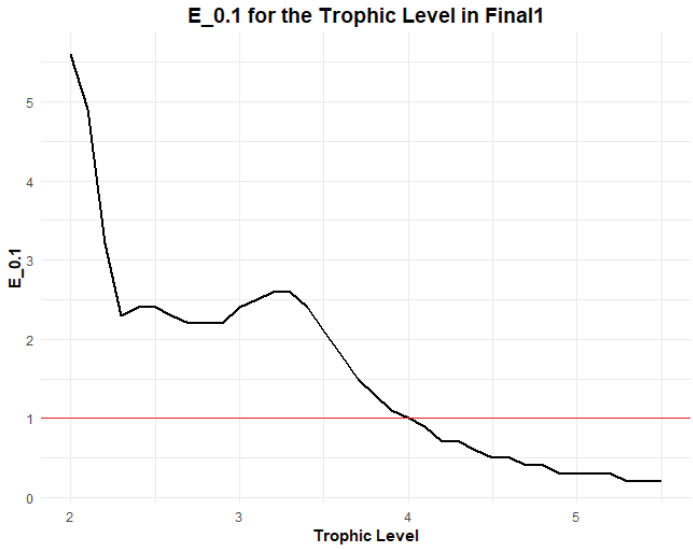


**Figure 11**: $E_{0.1}$ calculated by Ecotroph for the future Gulf of Lions ecosystem

With Ecotroph, I tested different fishing strategies by applying mE to specifics species. When analysing the landings while targeting only the SPFs (**figure 12a**), a clear bottom-up effects appeared. When increasing the fishing effort on SPFs, the SPFs biomass decrease in the ecosystem. With less SPFs available for the top predators, their B decrease, and then their landings (under the same mE) also decrease. This bottom-up effect confirms the essential position of the SPFs in the ecosystem, as their biomass directly impact the high TL ecosystem. Conversely, if the fisheries target only the top predators consuming SPFs (hake, anglerfish, European conger, Atlantic bluefin tuna, and the box "Pelagic fish (feeding on fish)"), no clear top down effect can be noticed (**figure 12b**): the different mE do not affects the catches of SPFs (TL between 3 and 3.5).

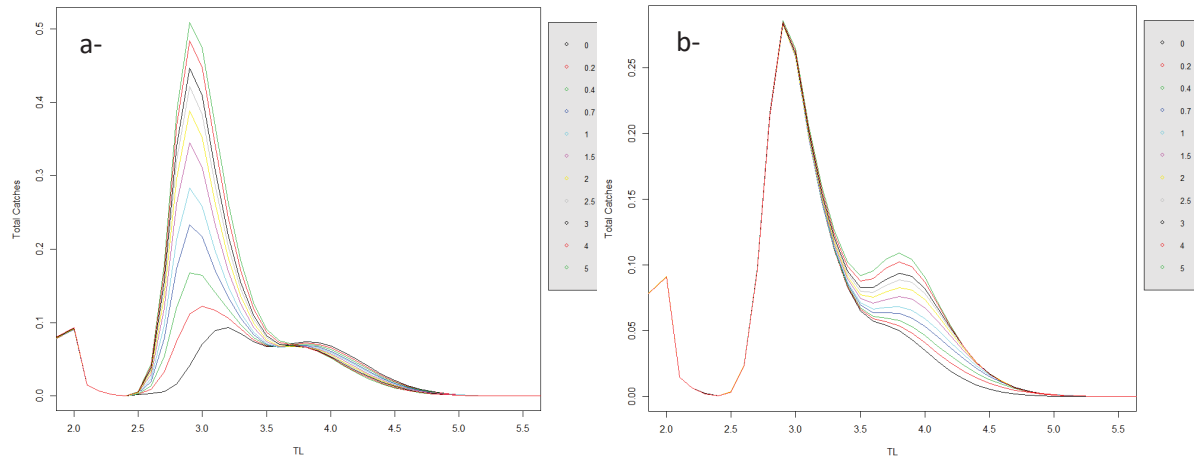



**Figure 12**: (a) Ecotroph's catches applying mE only to the SPFs and (b) catches applying mE only to top predators

# IV/ Discussion

## A – Reliability of the method developed in the study

### 1) Statistical relationship and quality of the dataset

No statistical relationship between the POP and the B has been found in the first step of the study. Several points may have limited my work. The first one was the quality of the dataset. I used data retrieved from stock assessments and Ecopath models. Some surfaces of the study area were not covered by any available model. I lacked data on the Mediterranean Sea especially, missing some wide regions, therefore losing spatial information.

Moreover, by using only POP and F to explain B the models were not able to reflect the past fishing pressure consequences. Indeed, an important inertia effect can occur, even when averaging the data on the 17 years period. The F was high when the abundance of fish was still high and, on the opposite, when a stock collapsed, the fishing pressure was restricted and lowered. Taking the case of the Bay of Biscay's European anchovy (ICES, 2018), which collapsed in the 2000's due to a past over exploitation (1980/2000), a moratory occurred in the late 2000's: the averaged B was abnormally low for the period, but the fishing pressure was

also low, due to the recent regulation the government put in place, drastically limiting the quotas. Rescheduling the F on the previous years was not appropriate, as each collapsed stock has its own dynamics. For instance, the overexploitation of the Bay of Biscay's European anchovy was old, and the F may be postponed by more than 10 years to reflect it; conversely, on the Catalan Sea the B followed the evolution of the F each year, without any delays. Other parameters were tested such as the temperature and the primary production but did not improve the relationship.

Finally, one of the major limits of the dataset came from the wide surface covered by many models. It lost spatial information's: each model only gave 1 biomass value, while the surface covered a large spectrum of POP values. For example, the stock assessment of the European anchovy in the Black Sea represented POP values from 0.05 to 0.82.

For both studied species, the European anchovy and the European pilchard, the data were widespread, impeding to fit any relationship. Every data's original model was checked, to value its reliability. I tested to remove models presenting past overexploitations or suspected high Illegal, Unreported and Unregulated (IUU) fishing. These modifications did not permit to fit any better relationship.

The widely spread data show that either an important environmental parameter has not been integrated in the preceding work from A. Schickele, biasing the POP values; or the local abundance is depending on specific conditions difficult to take into account in niche models, as local productivity or anthropogenic factor as pollution and overfishing, not directly influencing POP but abundance. Because Ecological Niche Models (ENMs) are based on environmental parameters only, they produce POP values and not directly abundance values, as they do not integrate these non-environmental parameters.

The work conducted with NLRQ was to test a hypothesis made during the study, when I observed the spread data: the values come from a large variety of ecosystems, each with their own specificities. Species abundance for a given POP could varied depending on the local productivity or the anthropic pressures for example. NLRQ give a relationship for each quantiles of the dataset. I obtained a relationship for the "low productive" areas, and a relationship for the "highly productive" area. By dividing the dataset in quantiles, the relationships were fitted on a few points only. This method should be reconducted, with a larger dataset.

### 2) Ecosystem modeling

By integrating future potential biomass of 10 species in an Ecopath model, I studied the sensitivity of the Gulf of Lions ecosystem and his food web to a range-shift of key species. The different levels and calibrations methods applied strengthen the study, considering uncertainty. The original model from Bănaru et al. (2013) showed a pedigree value (measure of reliability of the inputs in an Ecopath model) of 0.584, confirming that the inputs data essentially come from local surveys, and showing a certain solidity of the model.

However, some defaults were identified in the model (e.g. EE values too low for some forage species). The model can not be considered as a perfect representation of the Gulf of Lions, but an approximation to study the global ecosystem tendencies. Only 10 species were directly impacted by the global warming in the study and I followed the tendencies of the model. Still, it shows the potential roles and implications of these species in the future and shows the evolution of this specific ecosystem under those hypotheses.

The Ecotroph inputs values were retrieved from the Ecopath models. Their reliability therefore depended from the quality of the Ecopath model. Only the accessibility values came from expert knowledge. I conducted a sensitivity analysis on these values, changing the accessibility values by 10%, and following the variations of the Ecotroph outputs. With low evolution on every output, the sensitivity of Ecotroph to accessibility values was considered low in our study.

## B – Ecological interpretations

The future biomass for 2100 under the RCP 8.5 scenario, were calculated for the 10 studied species with the linear relationship hypothesis. They can't be considered the exact future values of biomass, but they reflect the tendencies due to the future distributions. The future B are forced by the future environmental conditions in the Gulf of Lions, i.e. the SST, its variability, the salinity and the primary production. 8 species over 10 show lower biomass values for the end of the century, with a potential collapse for the European sprat and the round sardinella. Lower future abundances involve physiological stress for the concerned species. which may have to adapt to this future situation, modifying their behaviours or their production.

When forcing Ecopath models with the future biomass, 4 species (i.e. the European sprat, the Atlantic horse mackerel, the common octopus and the common cuttlefish) presents EE values over their specific threshold value, meaning they are unbalanced. To fit in the future model, input parameters values must be adapted. These changes, applied during the 3 calibrations methods, reflects the possible modifications of the species or ecosystem dynamics necessary to balance the model. In this study, I adapted the productivity of the concerned species, the diet of its predators or the B of every other boxes. The future adaptations of every species and of the Gulf of Lions ecosystem to the future B are probably a mix of these 3 modifications possibilities, in between the 3 calibrations methods. Other parameters might change like the consummation of predators or the landings but were not considered in this study.

The European sprat and the round sardinella are 2 main forage species in the Gulf of Lions ecosystem. Their collapse may drastically change the diet of top predators and their B with the lowered bottom-up effect. These species may also go through severe stress and adaptation to survive in the ecosystem. The global diminution of SPFs biomass implies an important impact on the whole ecosystem. The second calibration methods of the first level reflect it, with a 3.5 times more important biomass reduction than when fixing the other boxes biomass. The B adaptation of all the boxes of the model lead to a large global B decrease to adapt to the small SPFs diminution. The European anchovy is the only species showing significantly higher future B. This modification may increase the intraspecific competition. However, SPFs species show similar diet. With the global diminution of SPFs, the European anchovy may not encounter any difficulties to find resources.

The cephalopods also show lower B values. They are essential parts of a few top predators, as dolphins, which may imply future diet-switch for those animals (coupled with the SPFs changes). Cephalopods are already over exploited. With smaller future B, cephalopods fisheries must be impacted, and may have to change. Finally, cephalopods are predators of SPFs. Their B diminution lowers the total predation pression on the SPFs, tempering the consequences when applying all the future changes.

The other species showing lower future B do not exceed their EE threshold value when forcing the model, meaning that the current ecosystem can support their changes. Still, an

increase in EE values imply less natural mortality (predation not included). They also may have to adapt to their future abundance, but do not need large adaptation.

The global ENA indices from the first set indicates the global tendencies the Gulf of Lions ecosystem may followed in the context of global warming. Every index (except the SOI) presents the same tendencies whatever the levels or the calibrations are. Thus, the Total System Throughput (TST) decreases with the global warming. The TST is a measure of the activity of the ecosystem, and of its growth and maturity (Saint-Béat et al., 2015). It is dependent to the total biomass in the ecosystem, which explains its more important sensitivity towards the second calibration methods: this calibration let the Ecopath software balanced the model modifying the B of every trophic boxes. It results in larger total biomass modifications, 3.3 to 3.5 times bigger, due to an important biomass decrease in organisms with TL inferior to 3. The TST reacts less to the 2 other calibration methods compared to the second one: 0.05% diminution for the final levels (all 10 species modified), first and third calibrations against 2.28% diminution in final levels, second calibrations. With only the SPFs and cephalopods biomass modifications, the TST (and thus, the activity and maturity of the ecosystems) does not seems impacted. The Average Path Length (APL) is a measure of the maturity and complexity of the ecosystem. It is also decreasing in the future ecosystem. A future particle of carbon must go through less trophic box to reach the top of the food web, with a simplified and shorter future food web.

The Ascendency (A), Capacity (C) and Overhead (O) are 3 indices interconnected (C = A + O), exposing similar variations in the future ecosystem. The A represents the organised part of the ecosystem, reflecting the activity of the system and its internal stability and resistance. The O is the unorganised part of the ecosystem, measuring its resilience as it buffers the external perturbations. C is the maximum A the ecosystem may reach, if the O was organised. The stability and sustainability depends of the balance between A and O (Ulanowicz, 2009), as the stability of an ecosystem depends of its capacity to endure internal changes and external pressures. By 2090-2099, those 3 parameters decrease. The global decrease of C will weaken the ecosystem, decreasing its internal resistance and resilience. Conversely, the ratio A/C increase. As A/C decrease with maturity, this evolution is coherent with the evolution of TST. The increase of A/C shows that A increase over O in the balance between these 2 parameters. It confirms the decrease of resilience of the ecosystem: with less reserves of unorganised parts, the return to stability after an incident is longer (Saint-Béat et al., 2015).

The Finn Cycling Index (FCI) decrease in the future ecosystem. The recycling linked with the detritus compartment of the ecosystem is essential. It concentrates a lot of organisms, and revalue matters and energies reintegrated in the system, that would be lost otherwise. The cycling can play an important role in the stability of the system, but must not be studied alone, as different cases show contrary results (Saint-Béat et al., 2015). In the study of Hosack et Eldridge (2009), cycling increased the resilience of the ecosystem. It seems that it also increases the internal resistance. This is in accordance with the precedent analysis of A, C, O and A/C: as the FCI decrease, the internal resistance and the resilience of the Gulf of Lions ecosystem also decrease.

The System Omnivory Index (SOI) slightly evolves in the study, only for the first and last levels. It increases, except for the last levels, third calibrations. The omnivory is a key parameter. It prevents the strong prey-predator links, and then avoid the sensitivity of species towards second extinction: if a prey disappears, the predators can find other food sources, as

they are not specialised. High omnivory also lead to a better exploitation of all the resources of the ecosystem. An important omnivory increase the internal resistance of the ecosystem. The biomass modifications and the diet calibrations may lead to important omnivory changes. In the end, SOI does not seem impacted in the study.

The evolution of the global indices shows that the Gulf of Lions ecosystem, under the B modifications of 10 species in the context of global warming, may tend toward a simpler and weaker state. Its resilience and its internal resistance against perturbations may decrease. It might be a smaller ecosystem, less active and with less interaction between species. The global diminution of B, mainly conducted by the SPFs biomass, must deteriorate the current ecosystem. The evolutions are slightly less important when combining all the species modifications, may be underlying some synergetic effects of the cephalopods, buffering the consequences of the SPFs changes. The first and third calibration methods show similar evolutions, linked with similar calibrations changes. The second calibration method show stronger evolutions (except for the A/C and the SOI), exposing the role of the B modifications: calculating new B for every trophic box in the second calibration methods, it shows a total B diminution 3 times more important than the B diminution of the 10 studied species.

Looking at the species indices, the evolutions seems proportional to the biomass changes. The bogue, the Mediterranean horse mackerel, the European pilchard and the common squids do not act importantly at the species levels.

The common octopus, even with its B changes, have very low difference percentages for KS indices and RTI. With a lower B, it stays as much impacting as in the current ecosystem. The European sprat and the round sardinella, with the highest B changes, see their RTI and both KS decrease importantly, especially for the third calibration methods, where they strongly decrease in the predator's diet. The decreasing KS indices (except the KS1 of the European anchovy) show that the studied species lose importance in the ecosystem. Their RTI decrease, exposing less impact on the ecosystem, negative (predating) or positive (being predated).

For the A, the C and the Throughput (T), the largest biomass changes expose the most important variations, carry out by the European sprat, the round sardinella, the Atlantic horse mackerel for the negative evolutions, and the European anchovy for the positive value. SPFs have more important variations than the cephalopods, explaining the differences in global indices between the second levels and the 2 others.

While for the global indices the calibrations methods changed importantly the extent of the evolutions with the second calibration methods exposing strong modifications compare to the 2 others, it is not the case for the individual's indices. Except a few very large differences, especially on the third calibrations methods on the KS indices and the RTI, all the indices show the same evolutions whatever the calibration method is. It shows a low sensitivity toward calibrations for the individual indices. The second calibration only impacts the global indices, linked with the more important global B diminution, and not the studied species implications. The diet and P/B modifications do not change much the results, at the species and the ecosystem levels.

With the global warming, the Gulf of Lions ecosystem may be weakened, less mature, resistant and resilient. In this context, fishing regulation and control may be essential to not aggravate the situation. The species with lower B in the future are priority target: the fishing pressure must be followed carefully for the European sprat and the round sardinella. Even if

the F is currently low, the future collapse of these stock might expose them. They may suffer important stress due to predation on their low B, that even small increase in landings may seriously impact them. The cases of the common octopus and Atlantic horse mackerel are alarming. Both are currently overfished (F = 0.520 for the Atlantic horse mackerel, and F=2.5 for the common octopus). Their decreasing B force to urgently restrict their fisheries. Conversely, the European anchovy must see its B increase in the future. Already an essential target in the Gulf of Lions as the second landing, it may have important positive economic repercussions.

Ecotroph shows that the top predators (TL > 4) are globally overfished. The bottom-up effects of the SPFs toward the top predators might become weaker in the future, with the global B decrease. Regulating the fishing pressure on those organisms is also essential. The TL between 3 and 4 have some reserves according to Ecotroph. This information is difficult to handle, as several species at these TL are not and will probably not be fished, biasing the actual F of the fished species. Still, the bottom-up effect implies to be careful with these organisms. If SPFs become over-exploited in the future, the collapse of these stocks may directly impact the top predators' stocks, aggravating the current overexploitations at TL superior to 4, and reducing their B and their landings. With its wide continental shelf and local productivity, the Gulf of Lions is one of the biggest Mediterranean Sea fisheries. Improving its regulation is a major current and future challenge.

# V/ Conclusions and perspectives

The global warming caused many physical and environmental changes in the ocean. Different marine species range-shifts have been stated during the last decades. Starting from these observations, this study aimed to evaluate the impacts those distribution changes may have on ecosystems, applying it to the Gulf of Lions ecosystem. It investigated a relationship between POP and B to pass from species distributions changes to local abundance modifications. Unable to fit a relationship with the data gathered, I continued the work with a hypothesised linear relationship to calculate the future biomass of the 10 studied species. The tendencies show a global B diminution, with collapse of the European sprat and round sardinella. The European anchovy is the only species that take advantage of the future environmental conditions of the Gulf of Lions and see its biomass increase.

I integrated the future B values in a Gulf of Lions Ecopath model to evaluate the food-web modifications induced by these few changes. Three levels of biomass applications with 3 calibrations methods were tested, adapting the P/B values, the predator's diets or the B values of other species. It changed the Gulf of Lions characteristics and functioning.

I worked on the Ecopath outputs, analysing ENA indices and building an Ecotroph model. ENA indices show a less mature, resistant and resilient ecosystem, exposing the future Gulf of Lions towards external and internal perturbations. The species with the largest B changes where impacting the most the Gulf of Lions. Ecotroph highlighted the B diminution and showed that overexploitation is an important issue in the Gulf of Lions for high TL fishes and some species at medium TL.

Global warming is known to take place in the 21$^{st}$ century, whatever the policy of international countries may be. My work shows that species range-shifts induced by the global warming

must impact Mediterranean ecosystems like the Gulf of Lions. Modifying the local abundance of some key species may transmits on the whole food web by cascades effects, impacting essential phenomenon like bottom-up effect. The Gulf of Lions ecosystem under the global warming induced B changes is less resistant and resilient, exposing it to external and internal perturbation that may become more and more frequent in the future. Fishing is sensible in the area as in many other Mediterranean Sea regions and the future changes may decrease landings and waken several stocks. Fishing pressure must be controlled, especially in this global warming context.

The study of the statistical relationship between B and POP may be reconducted. Improving the quality of the dataset, adding some future models or trying a different area may lead to a future relationship. Permitting future studies to pass easily from ENMs to local abundance, it offers a lot of opportunities as ENMs can covers wide areas, giving quickly a lot of abundances data.

I studied the tendencies of the Gulf of Lions ecosystem under the B changes of only 10 species. It can not be considered an accurate picture of the future ecosystem, as every other species of the model must react in different ways to the future environmental conditions. The study may be improved by integrating more species to the study, but it implies to run ENMs before. Adding more species gives a better idea of the global future tendencies, and may highlight different changes pattern, may be depending of the families or of the TL classes.

Another aspect that the future Gulf of Lions ecosystem may face is the arrivals of invasive species. The Eastern Mediterranean Sea is currently dealing with hundreds of Lessepsian species coming from the Red Sea with the Suez Channel. Some species are causing serious ecological and socio-economic issues, by competing with the endemics species or increasing predation pressure on forage species. Some species are suspected to threatened in a near future the Gulf of Lions, like the bluespotted cornetfish *Fistularia commersonii*, the pufferfish *Lagocephalus sceleratus* or the rabbitfish *Siganus luridus* (Daniel et al., 2009; Kletou et al., 2016). These species may be integrated in the future model, with ENMs giving their future B (with the linear relationship), and diet defined by expert knowledge. Ecopath may highlight their impacts on the endemic's species and the fisheries, amplified in the context of global warming.

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# Appendix

**Appendix I**: Details on the original work from A. Schickele

For full details on the study, see Schickele et al. (*under review*). Here are presented essential information for the construction of the model in supplementary table 1.

List of parameters: Sea Surface Temperature (SST), SST annual range (SSTr), SST monthly variance (SSTvar), log-transformed Primary Production (log_PP), Sea Surface Salinity (SSS), Sea Bottom Temperature (SBT) and SBT annual range (SBTr).

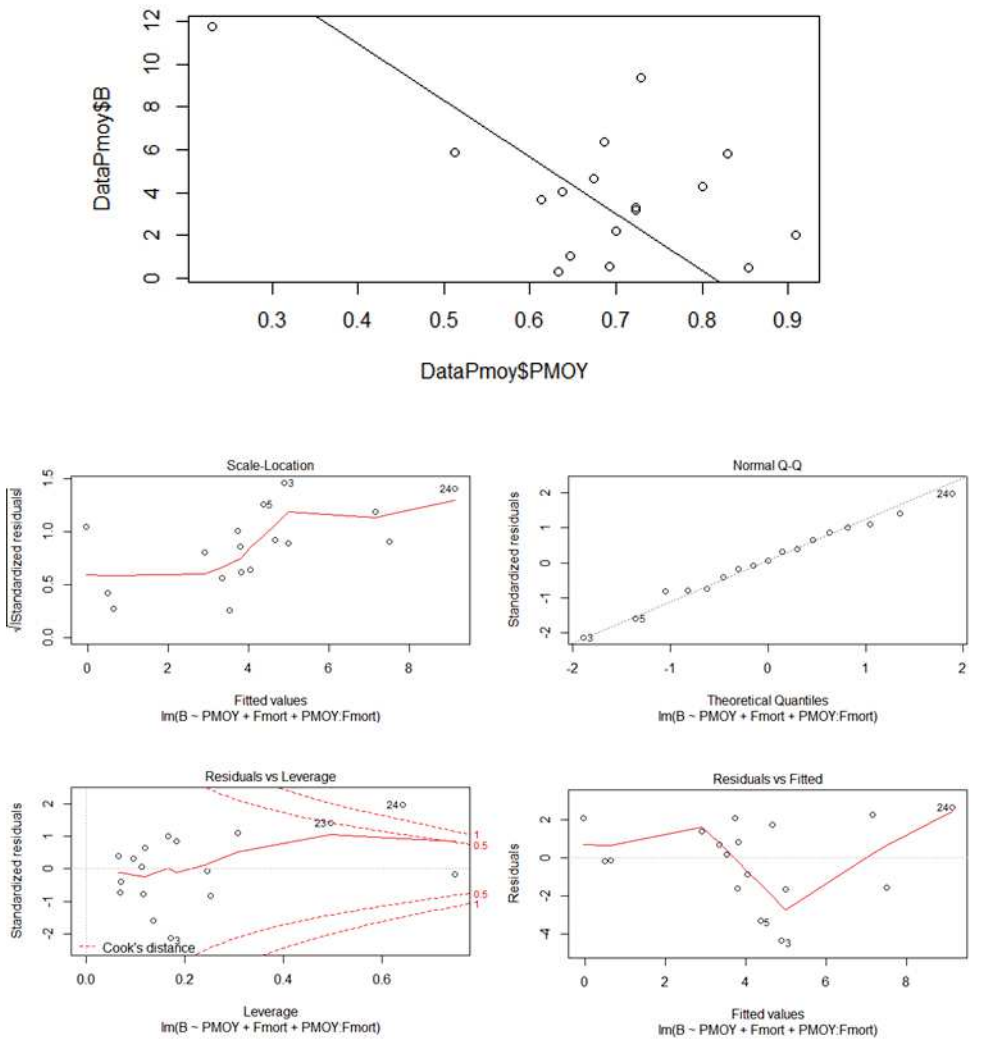
List of Models: Generalised Linear Model (GLM), Generalised Additive Model (GAM), Random Forest (RF), Non-Parametric Probabilistic Ecological Niche model (NPPEN), Multiple Adaptive Regression (MARS), Flexible Discriminant Analysis (FDA) and Artificial Neural Network (ANN).

**Supplementary table 1**: list of environmental parameters and models used for each species.

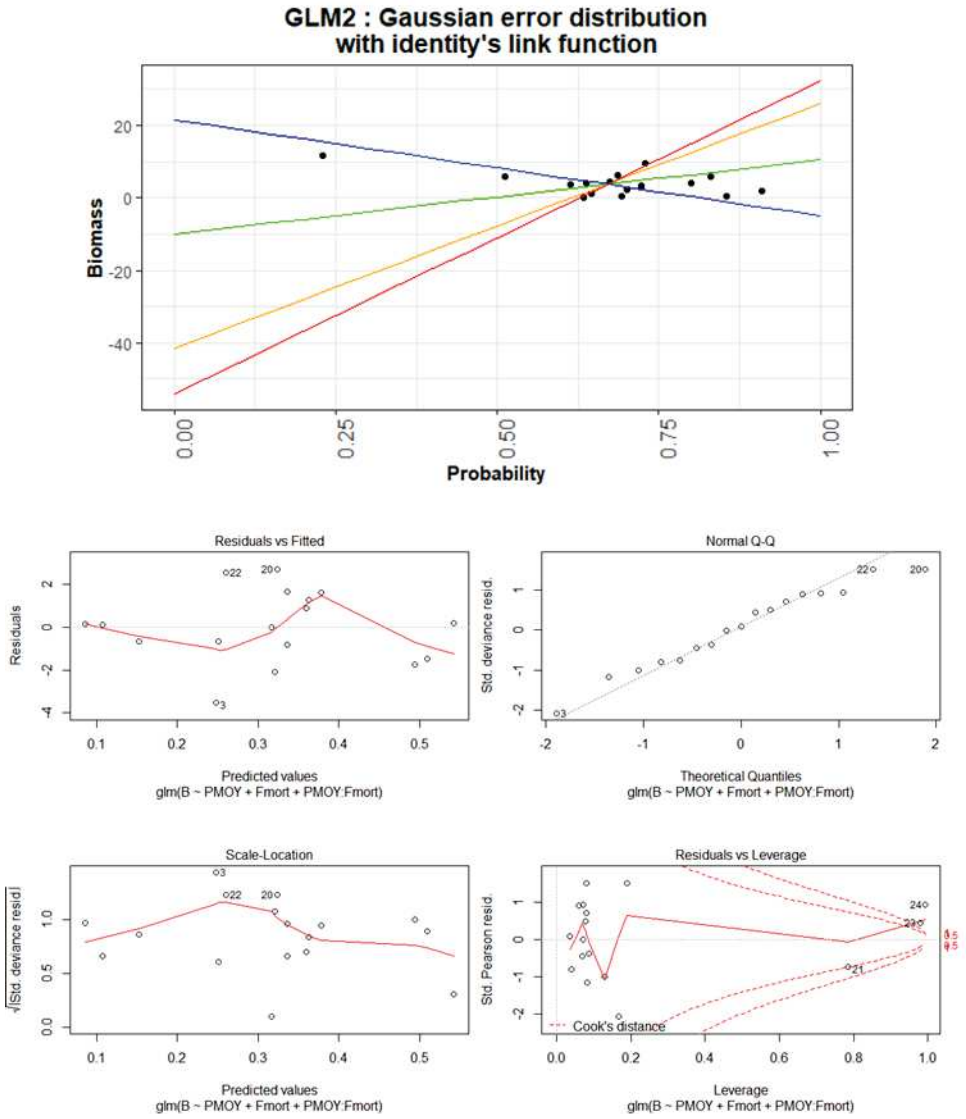
| **Species** | **Parameters** | **Models** |
|---|---|---|
| European anchovy | SST, SSTr, log_PP | GLM, RF, FDA, NPPEN |
| European pilchard | SST, SSTr, SSS | GLM, GAM, NPPEN |
| Atlantic horse mackerel | SST, SSTvar, log_PP | GLM, NPPEN |
| Mediterranean horse mackerel | SST, SSTvar, log_PP | GLM, RF, NPPEN |
| European sprat | SST, SSTr, log_PP | GLM, MARS, NPPEN |
| Bogue | SST, SSTr | GLM, ANN, NPPEN |
| Round sardinella | SST, SSTr, log_PP | GLM, RF, FDA, NPPEN |
| Common octopus | SBT, SBTr | GLM, GAM, ANN, NPPEN |
| Common cuttlefish | SBT, SBTr, SSS | NPPEN |
| Common squid | SBT, SBTr, SSS | ANN, NPPEN |

My study used the Probability of Presence (POP) values from Ecological Niche Models (ENMs) built for each species. The ensemble models are presented in supplementary table 1. They were calibrated following the method developed by Schickele et al. (*under review*), Leroy et al. (2014) and Bellard et al. (2016). This modelling framework includes (i) a multicollinearity assessment of the environmental parameters, (ii) sampling bias reduction through environmental filtering and (iii) pseudo-absence selection using the convex Hull method. The models were evaluated by means of the Continuous Boyce Index (CBI; Hirzel et al., 2006) and an analysis of the ecological relevancy of response curves. In the case of pelagic species (i.e. SPFs and the common squid), the POP values were limited to a bathymetry inferior to 300m to reflects the biology of studied species (Checkley et al., 2009). The distribution was expended to a minimum of 50km from the coast in cases of short continental shelf (e.g. Mediterranean Sea coast).

**Appendix II**: modeling the statistical relationship between Probability of Presence and Biomass for the European pilchard

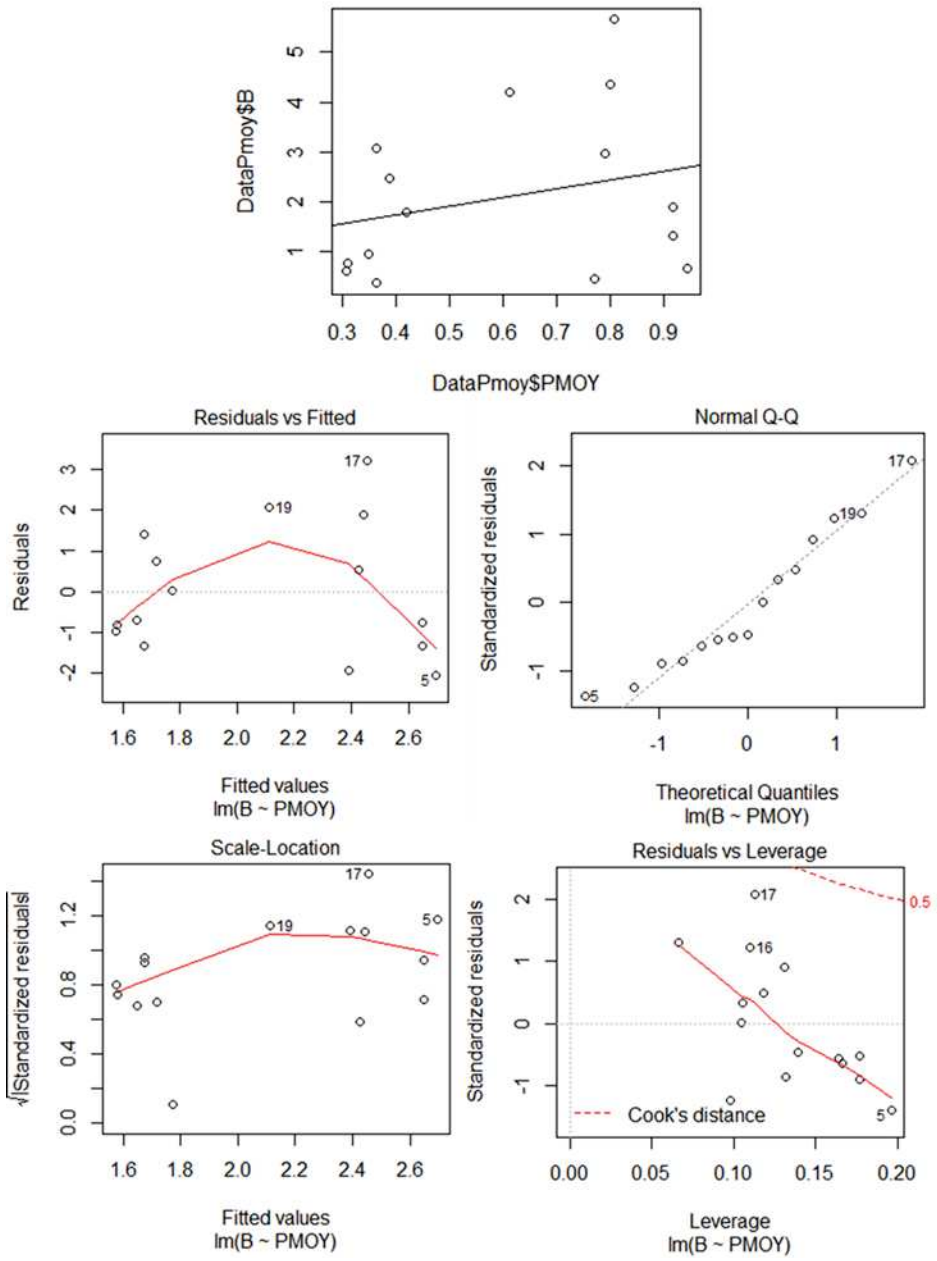



**Supplementary figure 1**: Linear Modeling and residual analysis for the European pilchard




**Supplementary figure 2**: GLM modeling for the European pilchard and its residual analysis

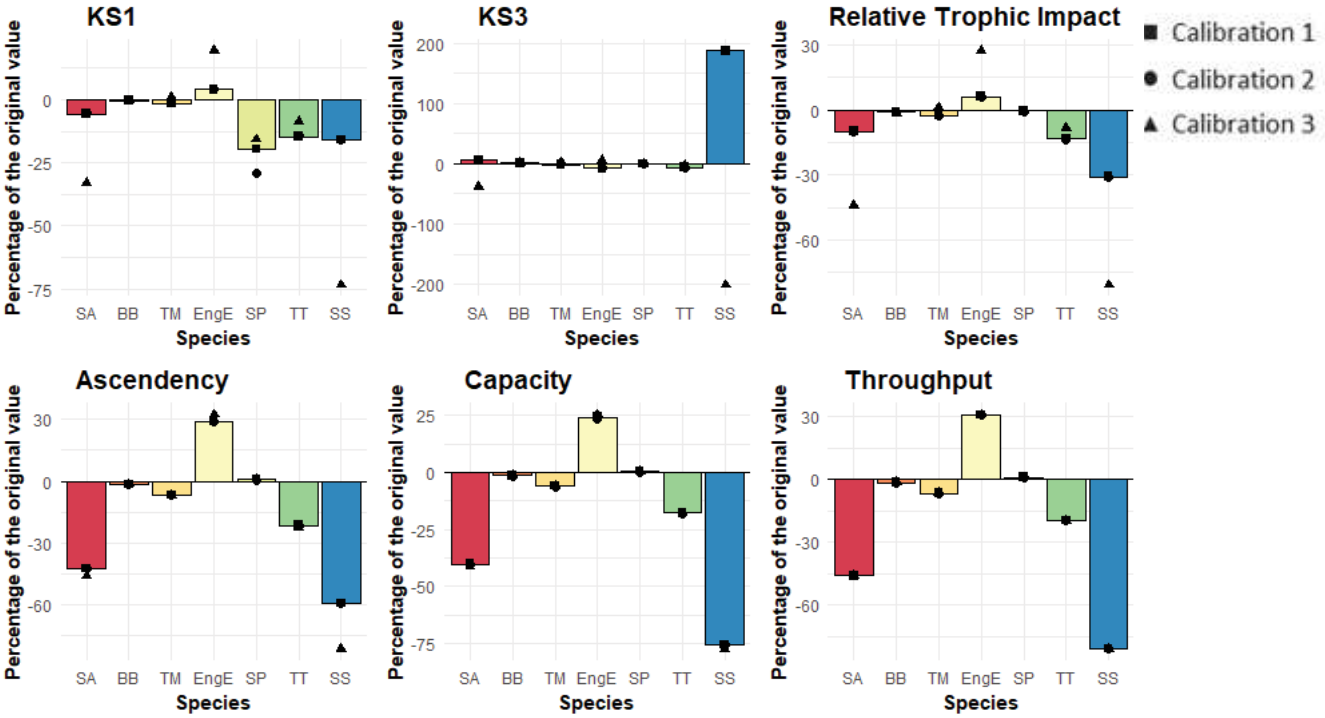
**Appendix III**: Linear model for the statistical relationship between the Probability of Presence and the Biomass for the European anchovy



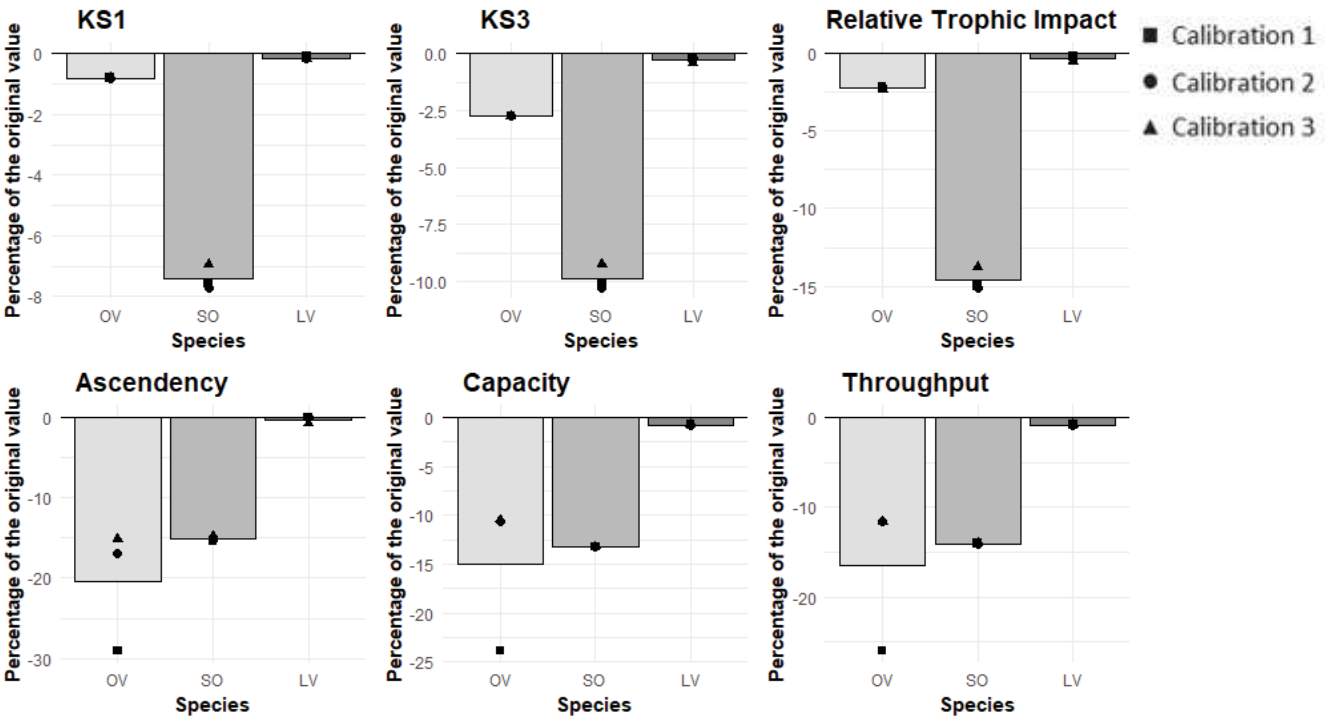
**Appendix IV**: new diet defined for the bogue in the Ecopath model

| Trophic Box | Original Diet | New Diet |
|---|---|---|
| Posidonia | 0.2 | 0.05 |
| Benthic Macrophytes | 0.33 | 0.05 |
| Mesozooplankton | | 0.05 |
| Macrozooplankton | | 0.260 |
| Worms | 0.02 | 0.02 |
| Benthic Crustaceans | 0.450 | 0.2 |
| Other Benthic Invertebrates | | 0.2 |
| European Pilchard | | 0.01 |
| European Anchovy | | 0.03 |
| Sardinella | | 0.02 |
| Other Planktonophagous Fish | | 0.1 |
| Sprat | | 0.01 |

**Appendix V**: Individuals ENA indices for the first and second levels




**Supplementary figure 3**: individuals ENA indices for the first level, integrating the future biomass of the Small Pelagic Fishes only

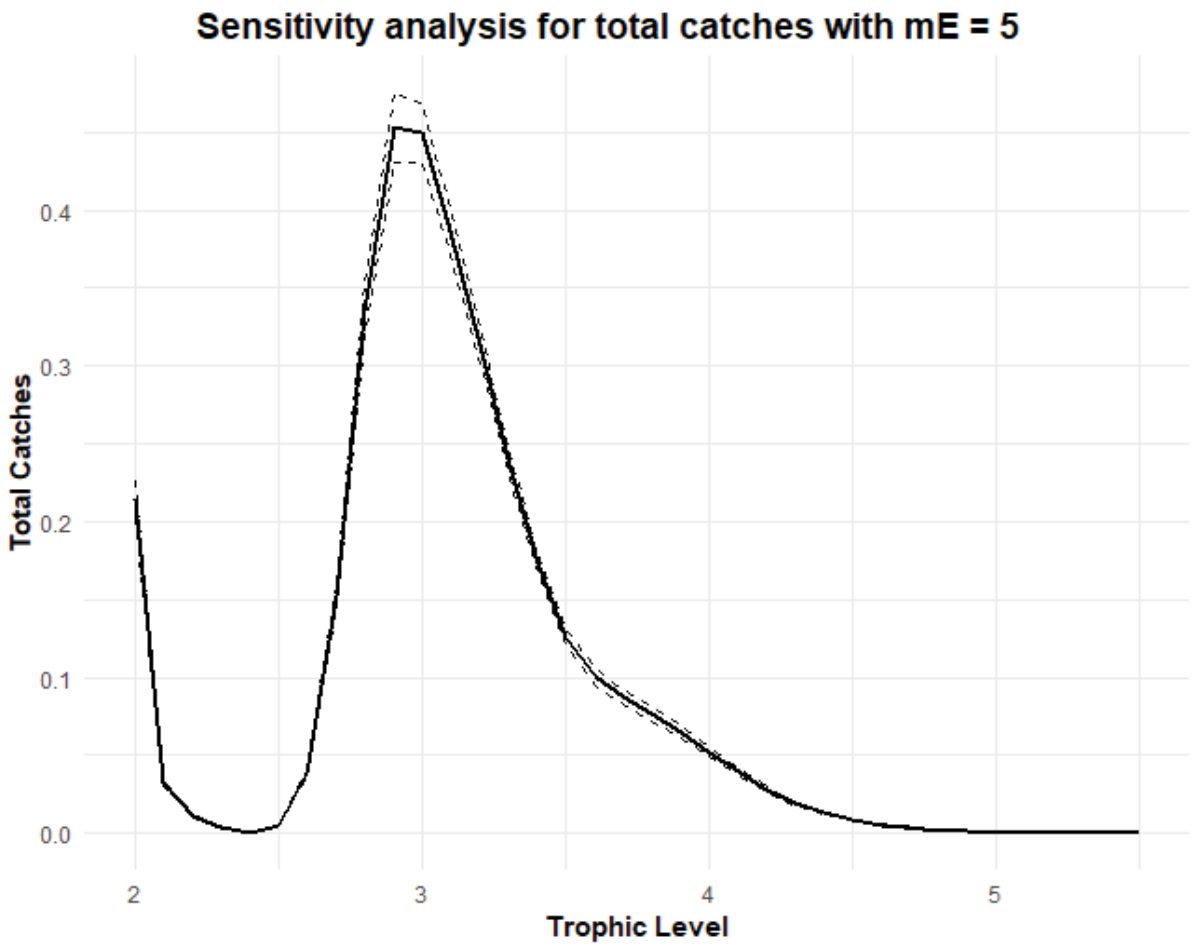



**Supplementary figure 4**: individuals ENA indices for the second level, integrating the future biomass of Cephalopods only

**Appendix VI**: Accessibility values used in Ecotroph, defined by expert knowledge

| Trophic Box | Accessibility |
|---|---|
| Pico-nanophytoplankton | 0 |
| Microphytoplankton | 0 |
| Microphytobenthos | 0 |
| Posidonia | 0 |
| Benthic Macrophytes | 0 |
| Microzooplankton | 0 |
| Mesozooplankton | 0 |
| Macrozooplankton | 0 |
| Gelatinous | 0 |
| Worms | 0 |
| Bivalves-Gastropods | 0,1 |
| Common octopus | 0,4 |
| Other Octopuses | 0,4 |
| Common Cuttlefish | 0,4 |
| Common Squid | 0,4 |
| Other Cuttlefish-Squids | 0,4 |
| Benthic Crustaceans | 0 |
| Lobsters | 0,4 |
| Echinoderms | 0,05 |
| Other Benthic Invertebrates | 0 |
| European Pilchard | 0,6 |
| European Anchovy | 0,6 |
| Bogue | 0,6 |
| Sardinella | 0,6 |
| Other Planktonophagous Fish | 0,2 |
| Sprat | 0,6 |
| Fish (feeding on plants) | 0 |
| Atlantic Mackerel | 0,6 |
| Mediterranean Horse Mackerel | 0,6 |
| Blue Whiting | 0 |
| Atlantic Bluefin Tuna | 0,6 |
| Hake Age | 0,6 |
| Atlantic Horse Mackerel | 0,6 |
| Anglerfish | 0,9 |
| European Conger | 0,9 |
| Poor Cod | 0,4 |
| Pelagic fish (feeding on fish) | 0,6 |
| Bentho-demersal fish (feeding on | 0,4 |
| Fish (feeding on benthic | 0,3 |
| Gilthead Seabream | 0,55 |
| Fish (feeding on polychaetes | 0,55 |
| Sea Birds | 0 |
| Dolphins | 0 |
| Whales | 0 |

**Appendix VII**: sensitivity analysis with total catches under an effort multiplicator of 5, varying the accessibility values by +/- 10%



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**Titre français** : De changements de distribution des espèces à modifications des réseaux trophiques : conséquences du réchauffement climatique en Mer Méditerranée

**Titre anglais** : From species range-shifts to food-web alterations: consequences of global warming in the Mediterranean Sea.

**Résumé** (1600 caractères maximum) :

Le réchauffement climatique impacte fortement la physique des océans, modifiant les courants, l'acidité et la température. Ces changements de conditions environnementales entrainent des changements de distributions des espèces, qui migrent vers les pôles afin de rester dans une gamme de température optimale. La Mer Méditerranée, zone riche en biodiversité mais présentant un caractère semi-fermé, semble particulièrement exposée.

Partant d'un précédent travail sur les changements de distribution de 10 espèces (7 petits poissons pélagiques et 3 céphalopodes), une relation statistique liant la probabilité de présence et l'abondance locale a été cherchée, afin de déduire les futures valeurs de biomasse des 10 espèces étudiées pour la décennie 2090-2099 dans le Golfe du Lion, sous le scénario de réchauffement climatique RCP 8.5. Ces biomasses ont été intégrées dans un modèle Ecopath, afin d'étudier la sensibilité du réseau trophique à quelques changements clés. Les sorties du modèle Ecopath ont été analysées à l'aide d'indice ENA (Ecological Network Analysis) et ont été utilisées pour paramétrer un modèle Ecotroph afin de suivre le rôle de la pêche dans ce contexte de réchauffement climatique.

La future diminution globale de biomasse des 10 espèces risque de fragiliser l'écosystème du Golfe du Lion, le rendant moins résistant et résilient. La diminution de l'effet bottom-up de ces espèces pourrait se répercuter dans tout le réseau trophique par effet cascade. La surexploitation des espèces de haut niveau trophique devrait être surveillée pour ne pas aggraver la situation future.

**Abstract** (1600 caractères maximum) :

Global warming is impacting ocean's physics, modifying currents, acidity and temperatures. These modifications of environmental conditions imply species range-shifts, as they tend to get closer to the pole in order to stay in their optimal range of temperatures. The Mediterranean Sea, a high pool of biodiversity but a semienclosed sea, seems particularly exposed.

From a precedent work stating the distribution changes of 10 species (7 small pelagic fishes and 3 cephalopods), a statistical relationship linking probability of presence and the local abundance have been investigated, to calculate future values of biomass for the 10 studied species for 2090-2099 in the Gulf of Lions, under the RCP 8.5 scenario. The future biomass were used to force an Ecopath model and evaluate the sensibility of the food-web to a few key modifications. Ecopath outputs have been analysed with ENA indices (Ecological Network Analysis) and have been used to parameter an Ecotroph model, to study the role of fishing in the global warming context.

The global future biomass decrease for the studied species may weaken the Gulf of Lions ecosystem, decreasing its resistance and resilience. The decrease of the bottom-up effect of the studied species may transmit to the whole food web through cascade effects. Overfishing on high trophic level species must be controlled, to not aggravate the future situation.

**Mots-clés** : changements de distribution, réchauffement climatique, Ecopath, Méditerranée, Réseau trophique

**Key Words**: range-shift, global warming, Ecopath, Mediterranean, food-web

* *Elément qui permet d'enregistrer les notices auteurs dans le catalogue des bibliothèques universitaires*